A Quantitative Assessment of Ra'ui (a Traditional Approach to Marine Protected Areas) on the Fishes and Invertebrates of Rarotonga, Cook Islands.

Sonja Lee Miller

A thesis submitted to Victoria University of Wellington in fulfilment of the requirements for the degree of Doctor of Philosophy in
Marine Biology

Victoria University of Wellington
Te Whare Wānanga o te Ūpoko o te Ika a Māui

2008

ABSTRACT

Ra’ui (traditional marine managed areas) in Rarotonga, Cook Islands, are a form of marine protected area re-implemented in the late 1990s when communities became concerned about declining fish and invertebrate stocks in the lagoon. In this thesis I quantified the effects of Ra’ui on fish and invertebrates.

First, for a single focal species of abundant reef fish *(Ctenochaetus striatus),* I developed a novel framework to incorporate environmental heterogeneity into a Control-Impact assessment of Ra’ui effectiveness using an index of habitat selectivity (Manly’s alpha) to ‘adjust’ the density of a reef fish by ‘preferred’ substrates. My results empirically demonstrated that substrate heterogeneity impinged upon the interpretation of MPA effects. This suggests that habitat heterogeneity should be quantitatively incorporated into analyses of MPA effects to provide a more robust and defensible set of inferences.

The novel framework was then used to assess the effects of Ra’ui on densities of other common reef fish and invertebrates, as well as fish functional groups. Averaged across all Ra’ui, a higher percentage of the invertebrate species (20%) had greater abundances inside Ra’ui relative to corresponding Control sites than fish species (15%). This may suggest spatial management is more effective for sessile organisms such as the invertebrates in this study.

Even when environmental heterogeneity was ‘controlled’ in my analyses, responses to Ra’ui were variable between species and sites, illustrating that factors other than environmental heterogeneity may be driving varying patterns of species abundances. However, for the broad-scale functional groups, there were indications of inverse relationships between predator and prey functional groups at 3 of the Ra’ui. I applied meta-analytical techniques to my data to assess whether there was an island-wide effect of Ra’ui on the densities of fish and invertebrate species, and functional groups. There was no evidence in the meta-analyses for an island-wide Ra'ui effect for any species or functional groups. However, analysis of covariance suggested there was an island-wide Ra'ui effect for a number of fish and invertebrate species. The body size of fish and invertebrates is another metric of MPA effectiveness that is expected to increase with protection. However, in determining an island-wide effect of Ra'ui on size, only two fish species, *Mulloidichthys flavolineatus* and *Stegastes nigricans*, had greater mean size in Ra'ui relative to Control sites, and *Siganus argenteus* was the only reef fish to exhibit greater maximum size in the Ra'ui. Two of the lagoon invertebrates (*Echinometra mathaei* and *Tripneustes gratilla*) and three of the reef-crest invertebrates (*Echinothrix diadema*, *Echinometra oblonga*, and *Trochus niloticus*) exhibited an island-wide positive response to Ra'ui for mean size. At individual Ra'ui sites, a number of invertebrates had greater mean and maximum size. Further, at individual sites, *M. flavolineatus* had greater mean size across the most Ra'ui (4 sites), again indicating that the site fidelity of a species may influence its response to protection.

Ontogenetic shifts in habitat use are known to occur in fish and invertebrates. For five fish species, juveniles used habitat differently to adults of the same species. Further, of the five species, only densities of both juvenile and adult *Acanthurus triostegus* exhibited a positive relationship with the proportion of their preferred habitat (juveniles: $r^2 = 0.44$, $p = 0.011$; adults: $r^2 = 0.46$, $p = 0.009$). Densities of adult *Ctenochaetus striatus* also increased linearly with the proportion of preferred substrate cover ($r^2 = 0.43$, $p = 0.035$). These results suggest that habitat within an MPA may be limiting for different benthic stages of an organism's ontogeny.

Some knowledge of the characteristics that underpin MPA effectiveness can aid in their design. Using commonly occurring fish and invertebrate species, I explored the effectiveness of individual Ra'ui using three separate metrics of effectiveness (the proportion of fish and invertebrates exhibiting 1) greater densities, 2) greater mean size, and 3) greater maximum size in Ra'ui relative to Control sites. Ra'ui area and total fish density in each Ra'ui were characteristics that best described the effectiveness of Ra'ui in enhancing mean fish and invertebrate size. The level of compliance with Ra'ui may also have some impact on Ra'ui effectiveness.

This study highlights the importance of incorporating environmental heterogeneity into assessments of MPA effects. Further, temporary prohibitions such as Ra'ui may be more effective for some species if certain conditions are met e.g., compliance is good, and the species Ra'ui are protecting / enhancing have high site-fidelity and high growth rates. These findings provide important information for fisheries and conservation managers (e.g., traditional leaders, governmental agencies, non-governmental agencies, communities) that will aid in better design of monitoring programmes and facilitate improved MPA design, not only in the Pacific region, but worldwide.

ACKNOWLEDGMENTS

Firstly, I'd like to acknowledge two of my great uncles who are no longer here, the late Tom McCulloch and the late George Miller. Uncle Tom, for supporting and encouraging me to go back to University, ngā mihi tino nui ki a koe. Uncle George, I'm extremely grateful to you for having continually supported me in my educational endeavours.

I respectfully thank the Koutu Nui in the Cook Islands, particularly Te Tika Mataiapo, Dorice Reid, for allowing, and supporting me in carrying out this research on the Ra'ui of Rarotonga. I'm also thankful to the staff at the Ministry of Marine Resources, particularly Ian Bertram, Kori Raumea, and Jo Anderson for helping me get the research going and for ongoing support during my time in Rarotonga. This thesis would not have been possible without the support of the Koutu Nui and the Cook Islands Ministry of Marine Resources. All work for this thesis was conducted under a Research Permit issued by the Cook Islands Office of the Prime Minister (Permit Reference Number 10/04).

I thank my supervisors, Jeff Shima and Nicole Phillips, for supporting me throughout this research, always being available, providing prompt advice and constructive feedback. I'd also like to thank Jeff and Nicole for the barbeques and pizza nights – they have always been a highlight of my time here in Wellington. You are great supervisors!

Thanks to Dr Shirley Pledger for her statistical expertise – I don't know what I would have done without your help! I'd also like to thank Dr Colleen Kelly for statistical advice.

Ngā mihi nui ki Te Rōpu Āwhina Putaiao, especially Liz Richardson and Dawn Reeves, and all of the Āwhina whanau. The aroha and āwhi provided by Āwhina have been invaluable to me over the past years. I'd also like to thank MAI ki Poneke at Victoria University of Wellington for reducing the isolation of PhD study.

To everyone who supported me in this research in the Cook Islands from back in 2001 when it was just an idea until now; Gerald McCormack, Judith Künzle, Pasha Carruthers, Anna Tiraa-Passfield, Ngatuaine Maui, Navy Epati, Vaitoti Tupa, Diane Charlie, Russell Thomas, Gwen Welland, Jacqui Evans, and staff at the Cook Islands Environment Service - meitaki ma'ata! To those who helped out by letting me use their kayaks or access the beach through their properties, especially, Anna and Charlie Tetevano, Jeannine Peyroux, staff at the Little Polynesian Hotel, and Noeline Burden- meitaki ma'ata!

Mona Matepi and Pat Fitzgibbon at WWF Cook Islands, thanks heaps for the cups of tea and chats! It meant a lot to me. Also to all the crew at Rarotonga Hash House Harriers – thanks for the friendly faces during my time on Rarotonga.

I'm especially grateful to Samuel Brown in Rarotonga – for support and friendship, particularly for helping me out in the field (you coped well with the bossy 'expedition leader'). Meitaki ma'ata e hoa!

I gratefully acknowledge the financial support provided by the following: the Foundation for Research, Science and Technology (Tūāpapa Pūtaiao Māori fellowship – Contract VUWX0302), New Zealand Agency for International Development (NZAID) (NZAID Postgraduate Field Research Award), Victoria University of Wellington (PhD Completion Scholarship, and 2 Faculty Research Grants from the Faculty of Science).

I'd also like to acknowledge my late Uncle Tom for helping to maintain and nurture the connection between the southern arm of the family and Wellington and New Plymouth whanau. Thanks to Aunty Marion McCulloch, and Linda McCulloch for providing me with what felt like a second home in New Plymouth. Kia ora also to Chargn Keenan and Wikitoria Keenan for their support of my research and return to tertiary study.

In SBS and the Science Faculty I'd like to thank the following staff – especially the Laydeez (Mary Murray, Patricia Stein, Delwyn Carter-Jarrratt, and Sandra Taylor), Michelle Sainsbury, Jo Long, Angela Flemming, Paul Marsden, Cameron Jack, Rachel Zhang, Belinda Tuari, Kasey Beveridge, and James Allen.

I'd like to thank my friends for their support prior to, and during my time at university, especially Sherrill Passau, Juliet and Greg Larkin, Barbara Bennett, Gina Huakau, Luke Mosley, Tim Ritchie, Richard Dukes (Dicky) and Belinda Smith, Mark Shafer, Sandra Bourguignon, Amber Bill, and Chris Fleck. I'd especially like to thank Helen Kettles for sharing her home with me for the past couple of years and coping super-well with my thesis-induced mania (especially near the end) - thanks heaps for your friendship and giving me a place to call home! To Kim Holland, Glen Mills and Sam Mills for giving me Gizzy mini-breaks (spas and barbeques, surfing, surf-casting at Nuhiti, and Muir's bookshop). I'd also like to thank my 'paper' supplier, Ann McCrone for her frequent e-mails. Chris Gibbons – thanks for the "breaks" and 'mean as' fussball games. Arohanui ki Lesley McLeod rāua ko Adele Whyte. Thanks so much to you both for your support, understanding, and friendship.

Gill Stotter, Ruth Highet, Liz Kemp, and Tessa Meek have also helped me produce this thesis (even if they didn't know it). I'd also like to thank a number of anonymous reviewers for their comments that have helped to improve the second chapter of this thesis. Thanks also to Darrin Drumm, Armagan Sabetian and Richard Hamilton for discussions and assistance prior to my returning to study.

Thanks to everyone in the Shima-Phillips lab group at Vic including Vanessa Hernaman, Chris McDermott, and David Aguirre. I'm especially appreciative of the time and effort Shane Geange, Anna Smith, Bionda Morelissen, and John van der Sman took to read over draft chapters and provide feedback. Shane Geange and Snout (aka Daniel McNaughton) were always only too happy to discuss stats with me – I owe you both a beer or two.

The people I've shared office space over the past years have made returning to university a pleasure. Marc Hasenbank – thanks for all the R help and also your friendship; Rudi Schnitzler – you've been there for me when things weren't going so well – thanks for your friendship!; Cliff Young – for thoughtful conversation - who would have thought you'd be post-docking it in Odense of all places!; David Hall - you saved me days of work with your "R" expertise); Bruce Dudley – so many cups of tea!; Nicolai Trümper – what would I have done without the chocolate, thought-provoking discussions, and software help?; Phil James – you sure make super-strong coffees!; Peter Martin – for the fussball thrashings; Shane Geange – you've always been keen to help out, and good company; and Bruce Norris – it's been a joy sharing an office with you, especially for the coffee, decent whisky (I didn't know what a decent whisky was until you taught me), more coffee, IT support (yup, I had to put that in), expanding my music repertoire, feeding me with delicious cakes and pasta bakes, and decent gut-wrenching laughs that have made the last 6 months of this process almost enjoyable!

Which reminds me, I must thank the following for early inspiration in my youth: the cast of Stingray (in 'Supermarionation'!), 'the Man from Atlantis' (aka Patrick Duffy, more famously known as Bobby Ewing in 'Dallas'), and Jacques Cousteau. In terms of music that has gotten me through, I'm indebted to Marvin Gaye, Shihad, SJD, Wilco, Jeff Buckley, and yes, a hangover from the music of my youth, A-Ha.

The "Supreme Champions of the World" (aka SCOTW) - the core crew deserve a special mention - Kristen (our beloved team leader), Dean, Kerry, Amy, and Bruce. Kristen, what would I have done every Thursday night if you hadn't invited me to join SCOTW at the Southern Cross music quiz, and Havana bar with the two for one mint and passionfruit daiquiris (it's healthy coz it's got greens and fruit in it!)

John – thank you so much for introducing me to the calming effects of sailing on Wellington Harbour, collecting kaimoana on the Wainuiomata coast, "gourmet" tramping, and highly competitive crib games (by the way, who's the champ?). Long may it go on! Your patience, love, and understanding have seen me through.

Finally, I'd like to thank my family; my sisters, Rachel and Jenny, for always having time for a chat and laugh on the phone, Paul Sirota for telling me to "start writing now!", wee Jozef Sirota for arriving into our lives, my bro Dave for being my dependable younger big brother, and my Mum and Dad for always being there for me. Without my family's love and support, this process would have been a lot harder.

Aroa Ra'ui, Rarotonga, Cook Islands

This thesis is dedicated to my parents, John and Vicky, my sisters, Jenny and Rachel, and my brother, David.

Table of Contents

List of Figures and Plates

List of Tables

CHAPTER 1: General introduction

Fishing, fisheries management, and conservation

There is increasing evidence that a combination of anthropogenic activities including fishing, pollution, and coastal development, are altering ocean ecosystems (PISCO 2007). Marine fisheries are in decline worldwide with over half of individual fish stocks fully exploited, a further 20% over-exploited, and over-fishing threatening the world's food security (Botsford *et al*. 1997, Garcia and Newton 1997, Watson and Pauly 2001).

Fishing is a consumptive (top down) process that can lead to major shifts in the trophic organization of fish and reef communities (Shears and Babcock 2002). Major changes can occur from fishing, including reduced species diversity and reduced abundances or loss of predatory species (Roberts 1995a). Fishing can lead to the loss of keystone species that sometimes results in major effects on reef processes, and the possible loss of whole functional groups, as well as affecting size-composition and life-history characteristics (Roberts 1995a). On a world-wide scale, fishing has led to major changes in the structure of marine food webs, evidenced by a shift in catches over the past 45 years from large piscivorous fishes to small invertebrates and planktivorous fishes (Pauly *et al*. 1998).

The impacts of fishing are not only restricted to global fisheries but also small island nations such as the Cook Islands in the South Pacific. Over-fishing, in concert with other human impacts such as pollution, is leading to reductions in fish stocks and suitable habitat (Sale *et al*. 2005).

Western management approaches to fisheries are generally based on conventional fisheries science theory, which was developed for the temperate, often single-species fisheries of the northern hemisphere (Botsford *et al*. 1997, Sale 2002). However, coral reef fisheries are generally multi-species fisheries, with marine communities that respond differently to fishing than temperate fisheries on which the bulk of fisheries science is based (Sale 2002). For example, major changes in community structure can occur as evidenced by regions in the Caribbean where intense fishing led to a single species of urchin subsequently dominating the herbivorous community (Lessios 1988, Jennings and Polunin 1996b). When the urchin suffered a mass mortality, there were no herbivores left in the system to keep algal abundances in check, resulting in no coral recruitment and death of existing corals (Hughes 1994, Jennings and Polunin 1996b, Pinnegar *et al*. 2000). Hence, existing fisheries management strategies where the focus is primarily on target fish populations and the use of concepts such as Maximum Sustainable Yield (MSY) and Maximum Economic Yield (MEY) use approaches that may not be well-suited to many reef fisheries in developing countries, and using such tools is likely not appropriate when applied to tropical reef ecosystems (Jennings and Polunin 1996b). Moreover, conventional fisheries management approaches rely upon the availability of long-term data sets and complex analyses (Sale 2002). Many developing nations lack the human resources and financial capacity to effectively implement this approach (Adams 1998). Consequently, many tropical reef fisheries are managed inadequately or not managed at all (Sale 2002).

There are alternatives to management based on conventional fisheries science for coral reef fisheries. One alternative is the use of marine protected areas, particularly when there are few data on which to base management decisions (Sale 2002, Botsford 2005). In addition, many countries reliant on coral reefs possess a wealth of knowledge with regard to managing the resource (Johannes 2002). Traditional forms of management based on indigenous knowledge, previously dismissed but now receiving more mainstream attention, are experiencing a renaissance (Johannes 1994, Young 2004). In particular, Polynesian cultures retain a great deal of indigenous knowledge that may provide innovative approaches to fisheries management (Adams 1998, Calamia 1999, Johannes 2002).

'Marine protected area' is a term that can refer to a number of protective mechanisms including strictly protected reserves, coastal management units including terrestrial and marine areas, or any kind of marine managed area (Agardy *et al*. 2003). It has generally been shown that marine protected areas result in increased size, abundance and diversity of marine organisms (Bohnsack 1998, Halpern and Warner 2002).

No-take marine protected areas differ from other forms of marine protection in that the harvest of marine life is prohibited (Roberts and Polunin 1991, Palumbi 2001). As well as conserving habitats and fish populations, there appears to be increasing evidence that no-take marine protected areas may sustain or increase catches in surrounding fisheries through what is referred to as 'spillover', via the export of larvae, and the export of adult biomass to areas outside the reserve (Balmford *et al*. 2004, Halpern *et al*. 2004). However, detection of 'spillover' requires very powerful sampling designs (Zeller *et al*. 2003).

Conservation and fisheries benefits are two common goals often stated for the design of marine reserve networks (Hastings and Botsford 2003, Neubert 2003). The design of marine reserve networks has much in common with terrestrial reserve design, incorporating aspects of the SLOSS (Single Large or Several Small) debate instigated by Diamond (1975). The results of models suggest that marine reserves may have benefits for fisheries when they are designed appropriately (Botsford *et al*. 2003, Hastings and Botsford 2003).

It is generally agreed that marine protected area design requirements vary depending on the desired outcome, whether that is primarily conservation or fisheries enhancement. It has been argued that reserves for conservation should be as large as possible, while reserves for fisheries enhancement should strive to maximise larval export out of reserve areas; fisheries reserves should be as small as possible but occupy a larger area of the coastline (Hastings and Botsford 2003).

In short, reserves for fisheries enhancement generally need to be smaller than those for conservation purposes, yet still large enough to maintain breeding populations while simultaneously maximising their edge to area ratio so that spill-over can occur across as large an area as possible (Hastings and Botsford 2003).

Connectivity, the linkage between local populations and processes, is an important consideration in the design of reserve networks, as the larvae (and often eggs) of most marine species have a dispersive pelagic stage (Roberts 1997). Hence, distant processes may have strong implications for local populations e.g., larvae spawned elsewhere may contribute to the persistence of populations in reserves (Roberts 1997, Lockwood *et al*. 2002, Sala *et al*. 2002). The implication is that marine reserves will not necessarily enhance species within their bounds if a critical bottleneck for a stage of the specie's life-history occurs outside the reserve.

Another design consideration for marine reserves relates to the displacement of fishers. Larval export from a marine reserve is required to offset increases in fishing pressure in adjacent areas (Halpern *et al*. 2004). That is, recruitment within the reserve needs to be over and above that necessary to compensate for the loss of the area to fishing, hence the size of the marine reserve is important (Halpern *et al*. 2004). However, caution should be applied to the use of marine reserves as unknown dispersal distances of larvae can mean that a reserve may end up disproportionately benefiting short-distance dispersing species, thus biasing a resultant community away from a 'natural' community (Botsford *et al*. 2001). If the implementation of a reserve results in a shift away from the natural community then it may not necessarily enhance surrounding fisheries for a particular suite of species.

Do marine reserves work?

There is a plethora of literature advocating the benefits of marine reserves for biodiversity and fisheries management yet it has been argued that there have been few adequately designed studies that clearly show fish density increases in marine reserves, and there are still conflicts about whether fisheries benefit from marine reserves (Sale 2002, Willis *et al*. 2003). Few studies have incorporated sampling designs to clearly determine effects. Hence, the evidence to support the use of marine reserves for fisheries management is still somewhat equivocal (Willis *et al*. 2003, Hilborn *et al*. 2004). However, marine reserves may be highly effective at increasing the size and density of fish within their bounds (Polunin and Roberts 1993, Jennings and Polunin 1997), but it is difficult to determine whether fisheries adjacent to marine reserves benefit (Palumbi 2001). Nevertheless, as mentioned previously, marine protected areas, especially for multi-species coral reef fisheries, are regarded as a viable alternative to conventional fisheries management (Sale 2002).

The role of life-history on the effectiveness of marine protected areas

The life-history of a species plays an important role in determining the effectiveness of spatial management tools such as marine protected areas. The stage at which any movement of a species occurs during its ontogeny has a large effect on the effectiveness of spatial management tools (Roughgarden *et al.* 1988). For species where little movement occurs, e.g., urchins, reproductive capacity is increased by spatial management (fishing mortality is reduced to nil assuming fisher compliance) as there will be little or no movement outside the protected area (Gerber *et al.* 2003). However, for highly mobile fish, marine protected areas may do little in comparison to conventional fisheries management tools (Hilborn *et al*. 2004) as the benefits afforded by marine protected areas decrease with increasing rates of adult movement (Gerber *et al.* 2003) with any movement outside protected area boundaries increasing vulnerability to fishing mortality. Therefore, spatial management tools may not be appropriate for species with high rates of juvenile and adult movement (Gerber *et al.* 2003)and consequently, spatial management (e.g., marine protected areas) is generally agreed to have the most effect on sedentary or sessile fish and invertebrates (Botsford 2005, Parnell *et al.* 2005). As many fish and invertebrate species on coral reefs conform to this life-history (i.e., sessile / site-attached adults), spatial management via protected areas may be a good approach (Hastings and Botsford 1999).

However, fisheries benefits may not necessarily result from marine protected areas as evidenced by the work of Ashworth *et al*. (2004) in Egypt, who concluded that for sedentary molluscan invertebrates such as Tridacna species, there was little evidence for potential spillover. Thus, any benefit to fisheries would depend on greater larval production as a result of no-take zones (Ashworth *et al*. 2004). Nevertheless, invertebrate fisheries in coral reef environments are usually located in shallow reef habitats that are easily accessible and therefore vulnerable to exploitation from over-fishing (Drumm 2004). Hence marine protected areas may prevent over-exploitation but there may be few, if any, fisheries benefits.

Another aspect of life-history particularly relevant to temporary marine protected areas is growth rate and age at maturity. For a temporary protected area to increase the reproductive output of a species, the closure should at least provide the species enough time to reach maturity and reproduce. For fast growing, short-lived species, species recovery may only take a few years in a protected area (Gell & Roberts 2002), which may be an adequate period of temporary closure if the aim of the closure is to increase stocks for harvest. However, for longer-lived, slower growing species, it would take longer for a species to reach its age at maturity (Gell & Roberts 2002), and consequently, any temporary protected area would at least need to be in place long enough for this to occur. Therefore, consideration of the life-history of any species to be ‘protected’ is a vitally important for temporary marine protected areas.

Marine reserves as a ‘traditional’ management tool for coral reef ecosystems

Coral reefs are highly diverse marine ecosystems yet more than half of the world’s coral reefs are threatened by human processes (Al-Jufaili *et al*. 1999, Moberg and Folke 1999), particularly over-fishing, which decreases the capacity of coral reefs to be productive or even sustainable (Roberts 1995a, Sale 2002). Although coral reef fisheries may contribute to only a small proportion of the global commercial fisheries catch, they remain a vital source of food and livelihood for many people, particularly in developing countries (Pauly *et al*. 2002, Sale 2002, Bellwood *et al*. 2004).

Coral reef ecosystems in the Pacific remain an important, if not vital resource for Pacific peoples, providing food and income (Overton and Thaman 1999, Samou 1999, SPREP 2001). Various forms of marine management based on observations over generations and learning from the past were in place throughout the Pacific pre-colonisation, and many of these systems are still functioning today, for example taboo in Fiji and Kiribati, Ra'ui in the Cook Islands, and rāhui in the islands of eastern Polynesia such as Moorea and Tahiti (Johannes 1994, Taniera 1994, Adams 1998, Veitayaki 1998, Barclay 2001, Churcher-Hoffman 2001, Young 2004). Similarly, in New Zealand, taiāpure (locally managed marine areas), mataitai (reserved coastal marine areas for marae use), and rāhui (prohibitions, see definition below) are present day marine management tools that can be used by an iwi (tribe) within their rohe moana (coastal area). Although indigenous knowledge systems have historically been dismissed by the western world (Barclay 2001), the last 20 years has seen a renaissance of community-based marine resource management in the Pacific Islands (Johannes 2002).

In New Zealand, rāhui is a means to prohibit a certain human activity from taking place or continuing (Mead 1984). A common type of rāhui is the conservation rāhui, often described as having 'no teeth', or being mild (Mead 1984). It is used in New Zealand, and also the Cook Islands in the form of Ra'ui, to protect resources derived from water or the land and involves restricted access or closed seasons to allow resources to regenerate (Barclay 2001).

Ra'ui in the Cook Islands

Definition

Ra'ui is defined in the Cook Islands Maori dictionary as '1. A sign, usu, leaves on a branch set in place by the owner of a piece of land or water reserving it or its produce for his own or some special use; a prohibition. 2. Erect a ra'ui restricting the picking of fruit etc.' (Buse and Taringa 1996). Last century saw diminishing use of Ra'ui in the Cook Islands, with the last Ra'ui on Rarotonga used sometime in the early 1970s (Churcher-Hoffman 2001). However, in the late 1990s Ra'ui were reinstated by the Koutu Nui (council of traditional leaders) to protect declining stocks of various resource species in the lagoons (Ama 2003).

Ra'ui have no legal basis (Reid 2000), and are not permanent with various Ra'ui in the Cook Islands having different periods of closure (Table 1.1). With increasing pressures on the lagoon and marine resource species in Rarotonga, Ra'ui may play a role in the sustainable management of key marine species. The present Ra'ui on Rarotonga can be viewed as a rotational harvesting strategy for a multi-species fishery. The Ra'ui may not only provide fisheries benefits but also provide benefits to tourism, and one of the Ra'ui is now permanent (Ra'ui Motukore). However, there is little quantitative information regarding the degree of fishing outside the Ra'ui and the level of compliance within Ra'ui.

Table 1.1. Characteristics of the 6 Ra'ui around Rarotonga (K. Raumea pers comm., Ponia and Raumea 1998, Ponia *et al*. 1998, Raumea *et al*. 2000a, b, Churcher-Hoffmann 2002, Saywood *et al*. 2002). NA = not applicable. *Tikioki Ra'ui (which originally occupied a greater area of the lagoon) was lifted on 1st February 2000 except for a smaller area, which was declared a permanent marine sanctuary (Ra'ui Motukore).

Ra'ui	Area (ha)	Mean depth (m	Date implemented	Date last opened	Length of opening	Status at time of surveys (2005)
Akapuao	35	1.7	Feb 2000	NA	NA	Closed to harvest
Aroa	16	1.0	May 2000	Not lifted	NA	Closed to harvest
Aroko	47	0.7	Feb 1998	Feb 2000	1 day	Closed to harvest (seasonal harvest of select species permitted)
Tikioki	3.3	2.6	Feb 1998	Not lifted*	NA	Permanently closed to harvest from Feb 2000 (Ra'ui Motukore)
Matavera	5	0.5	Feb 1998	Feb 2000	1 day	Closed to harvest
Parliament	13	0.7	During 2000	2003	1 month	Closed to harvest

Unfortunately, many traditional systems throughout the Pacific are being eroded for a number of reasons including the adoption of cash-based economies, the breakdown of chiefly authority and the introduction of new legal and political systems (Matthews *et al*. 1998). This has led to the suggestion that traditional management systems need to be re-evaluated to handle changing lifestyles, increased commercial fishing, growing populations and degradation of habitats (Matthews *et al*. 1998). To some degree, this is already happening with the Ra'ui in Rarotonga and according to Johannes (2002), the Ra'ui are a form of experimental management that is expected to result in improved Ra'ui design.

What is needed to advance our understanding of marine reserve performance?

The effectiveness of Ra'ui (or any managed marine area) is directly related to the life-histories of those species targeted for harvest. The temporal, spatial, and seasonal extent of the Ra'ui may be optimised to better sustain key resource species such as the pa'ua (Tridacna species), and rori (Holothuroidea) based on a better understanding of the life-history of each of these species. For example, short-lived and/or rapidly recruiting species might require shorter and/or more frequent closures to recover from harvests than longer-lived, slower growing / maturing or slower recruiting species.

My research will quantitatively investigate the effects of the Ra'ui of Rarotonga on fish and key resource invertebrate species. Few studies have examined such effects, particularly in the context of a network of temporary closures (i.e., Ra'ui, as opposed to permanent marine reserves). The Ra'ui of Rarotonga provide a unique opportunity to study these effects.

This study also provides an opportunity to try and avoid some of the problems with sampling design found in previous studies (see Willis *et al*. 2003). The data in my study comprise a single 'snapshot' in time, and consequently this limits generalisations and inferences that can be made based on my single large dataset. However, my ecological surveys sample replicate pairings of 'Control' and 'Ra'ui' sites, and I develop and implement a new approach that attempts to statistically evaluate the potential effects of natural environmental variability (i.e., a typically unexplored source of variation that may confound estimated 'reserve-effects' in most existing studies, particularly Control-Impact assessments).

My study was conducted with the consent and support of the Koutu Nui on Rarotonga, and in close association with the Cook Islands Ministry of Marine Resources (MMR). Results are expected to assist with management of the lagoon fish and invertebrate resources on Rarotonga.

Study Site

The Cook Islands comprises 15 islands located in the South Pacific Ocean, lying roughly north-east of New Zealand between latitudes 8°-23°S and longitudes 156°-167°W (Drumm 2004) (Figure 1.1). The main island, Rarotonga, (my study site) with a land area of 6719 hectares, is located in the Southern group of islands and is a volcanic high island surrounded by a shallow lagoon fringed by a narrow barrier reef (Wood *et al.* 1970) (Plate 1).

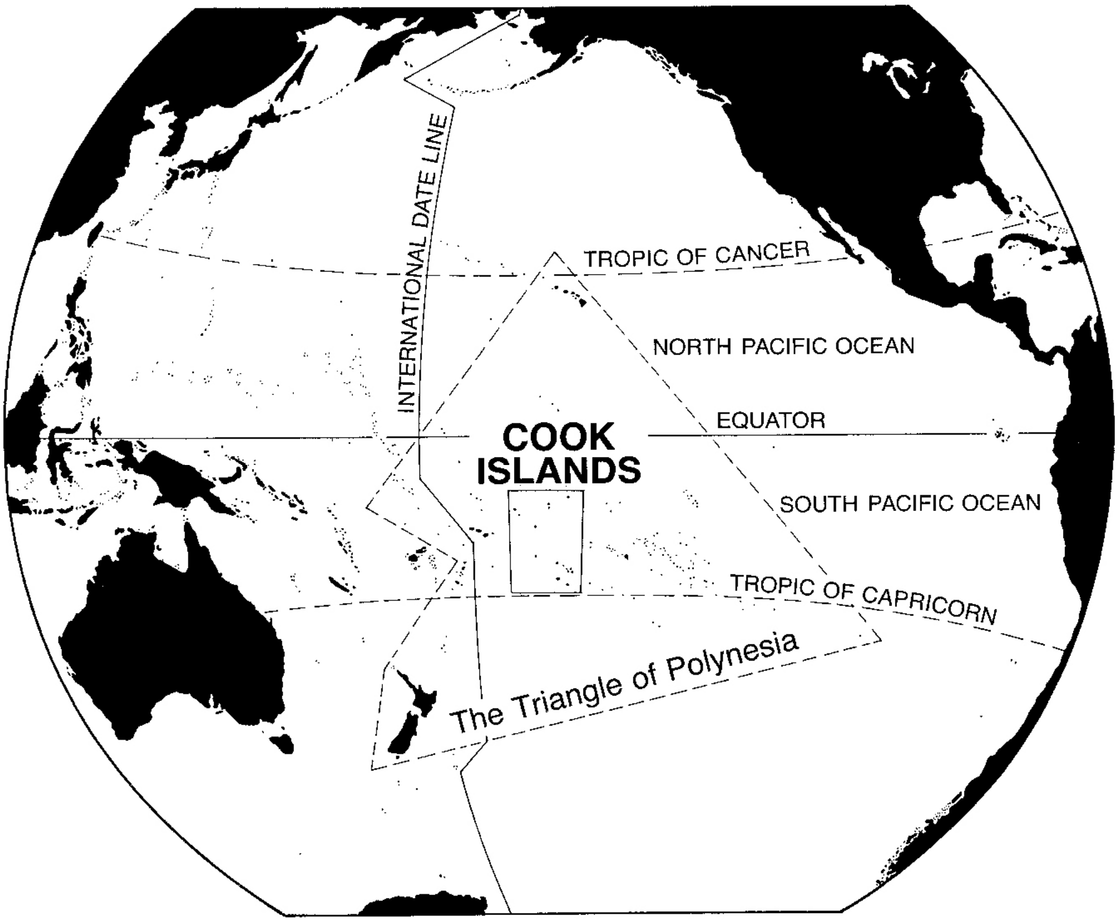


Figure 1.1. Location of the Cook Islands (map provided by G McCormack and J Künzle, Cook Islands Natural Heritage Project).

The climate in the Cook Islands is tropical, characterised by warm temperature, high humidity, moist winter months (June – September) and wet summer months (December – May) (Leslie 1980). The mean annual temperature on Rarotonga is

24 °C, with a mean annual relative humidity of 84% and, mean rainfall in winter of 425mm and 939mm in summer (Leslie 1980).

The lagoon is wider and deeper on the windward side of the island (between the south-east and west side) and narrower and shallower on the leeward side (between the north-west and east side). Tides on Rarotonga are semi-diurnal and small with a range of 0.3 metres on neap tides and 0.8m on spring tides (Gibbs *et al*. 1971).

Plate 1. Aerial view of Rarotonga from the south-east corner (Muri) looking west. Photograph courtesy of Ewan Smith, Cook Islands.

The Ra'ui of Rarotonga provide a unique opportunity to investigate the effectiveness of marine protected areas, in the context of a 'network' of temporary closures. To advance our understanding surrounding the performance of marine protected areas, my thesis is structured as follows:

Thesis structure

Chapter 2: Effects of substrate heterogeneity on estimates of density of a reef fish: Implications for assessments of marine protected areas

Chapter 2 specifically addresses one of the potential biases (habitat heterogeneity) that may arise from an implicit assumption of many researchers that chosen Impact and Control sites are 'roughly equivalent'. A single, ubiquitous reef fish species, Ctenochaetus striatus, is used to evaluate the effects of Ra'ui. The framework used for this work is a simple Control-Impact design, supplemented with species-specific estimates of habitat use and availability. This supplemental information is used to adjust estimates of fish density, and facilitates empirical evaluation of potentially confounding effects of habitat heterogeneity.

Chapter 3: Fish, invertebrate, and functional group responses to Ra'ui

The novel method to incorporate habitat heterogeneity into the analysis of Ra'ui effects developed in Chapter 2 is applied to other fish and invertebrate species to investigate responses to Ra'ui. The effects of Ra'ui are determined across functional groups for fish. I assess whether there are any notable patterns in the response of select species or functional groups to Ra'ui at each site. Using meta-analytical methods I also assess whether there is an island-wide effect of Ra'ui for any of the species or functional groups examined.

Chapter 4: Spatial variation in size-structure of key resource species as an indicator of Ra'ui effectiveness

For a subset of species for which I have representative and robust estimates of size-structure, I assess whether mean and maximum size (which can be used to infer estimates of natural growth and mortality) varies between Ra'ui and Control sites. I incorporate substrate heterogeneity into analyses of size distributions for five commonly occurring fish species. Habitat use can change over the course of an organism's ontogeny; consequently, habitat availability may determine the abundances of organisms during a particular stage of their ontogeny. I assess separately whether juveniles and adults use habitat differently. I then determine whether the amount of preferred substrate locally available shapes juvenile and adult densities.

Chapter 5: Site specific analyses of Ra'ui effects

In this chapter I explore the effectiveness of individual Ra'ui, obtaining separate estimates of 'effectiveness' for (1) effects on local abundance, (2) mean size, and (3) maximum size. I also explore some of the traits of Ra'ui that may shape variation in their effectiveness.

Chapter 6: General discussion / conclusions

Chapter 6 provides an overall synthesis of my thesis findings. I discuss the implications of my findings for Ra'ui, and marine protected areas. Recommendations are made for the assessment of MPAs (particularly those in tropical regions), which may assist in optimising the management of tropical fish and invertebrates for both conservation and fisheries purposes.

CHAPTER 2: Effects of substrate heterogeneity on estimates of density of a reef fish: implications for assessment of marine protected areas

ABSTRACT

Many estimates of 'marine protected area (MPA) effects' may be confounded by heterogeneity in environmental features (e.g., available substrate, habitat complexity) between 'Impact' (i.e., MPA) and 'Control' sites. However, the magnitude and extent of such confounding is generally unknown. Here, I explicitly explore the effects of substrate availability on estimates of MPA performance. I estimated: 1) abundance of the reef fish, *Ctenochaetus striatus*, 2) available substrate, and 3) substrate selectivity (Manly's alpha) of *C. striatus* within 6 'Ra'ui' (traditionally managed MPAs) and 6 paired 'Control' sites on the island of Rarotonga. I used a two-factor analysis of covariance (ANCOVA) model with 'useable substrate' as the covariate to test for an overall effect of Ra'ui. I used logged response ratios to evaluate putative effects of MPAs separately for simple counts recorded on my sampling transects, and for 'preference corrected' densities, where substrate types were weighted by an index of habitat selectivity (Manly's alpha). I contrasted both my simple and 'preference corrected' densities at each site with ANCOVA models. My results suggest that adjusting for substrate availability may significantly alter perceptions of the effects of Ra'ui on *C. striatus*. My framework allows estimates of effect size, a metric useful for assessing MPA effectiveness, and in concert with my ANCOVA models, provides a stronger assessment of MPA effects. Further, I conclude that substrate effects (or more generally, environmental heterogeneity) should be incorporated into future

assessments of MPA effectiveness, and this work describes one potential framework to accomplish this.

INTRODUCTION

Marine protected areas (MPAs) are widely used as tools for both conservation and fisheries management (Roberts *et al*. 2001; Sale 2002; Hastings and Botsford 2003; Cinner *et al*. 2006). Good estimates of MPA effectiveness are important for adaptive management and decision-making. The predicted effects of marine protection are that density, size, diversity and biomass of organisms will increase within MPA boundaries (Roberts 1995b; Jennings *et al*. 1996b; Russ and Alcala 1996; Wantiez *et al*. 1997; McClanahan *et al*. 1999; Tuya *et al*. 2000; McClanahan and Arthur 2001; Claudet *et al*. 2006). The general inference therefore is that reserves often have 'positive effects' in the context of conservation and fisheries management.

The assessment of MPA effects typically requires an estimate of 'baseline' conditions; for example, how many fish would be expected in the (theoretical) absence of an established MPA? However, in contrast to manipulative field experiments, the assessment of MPA effects typically cannot be effectively replicated. Accordingly, a number of approaches have been proposed to address difficulties associated with assessments of unreplicated interventions such as the implementation of MPAs e.g., Before-After (Box and Tiao 1975), Control-Impact (Osenberg and Schmitt 1996), Before-After-Control-Impact (Green 1979), and, Before-After-Control-Impact-Paired-Series (BACIPS) (Stewart-Oaten *et al*. 1986) study designs. Although a BACIPS study is considered the best for detecting the effects of unreplicated interventions, such as MPAs, there is typically little opportunity to implement this study design for a variety of reasons (see Osenberg and Schmitt 1996 for further discussion).

Limited opportunities to implement optimal assessment designs results in a preponderance of Control-Impact studies used to assess the effects of MPAs (Cole *et al*. 1990; Roberts 1995b; McClanahan *et al*. 1999; Tuya *et al*. 2000; Halpern 2003; Westera *et al.* 2003; Osenberg *et al*. 2006). For such studies, the intervention site (i.e., the MPA, or 'Impact' site), is assumed to be independent of a nearby Control site, which is selected as a point of comparison to represent the state of the natural system that would have existed had the intervention not been implemented (Osenberg and Schmitt 1996; Osenberg *et al*. 2006). However, Control-Impact studies confound effects attributable to the intervention with natural spatial variability in ecological systems (because no two sites are ever 'identical'; Osenberg and Schmitt 1996).

Sites (both Control and Impact) vary for many reasons, and this can lead to erroneous inferences of MPA effects, especially when siting is non-random (Osenberg *et al*. 2006). Despite the quantity of evidence (primarily from Control-Impact assessments; Halpern 2003), which suggests positive local effects of MPAs, some researchers (and managers, and fishers) continue to highlight limitations of existing assessments (Osenberg *et al*. 2006), raising questions about the actual effectiveness of MPAs as a tool for management and conservation (García-Charton and Perez Ruzafa 1999; Sale 2002; Willis *et al*. 2003).

One important factor that can produce spatial variability in marine organisms is habitat availability, which has been shown to influence species abundances (Bell and Galzin 1984, Pulliam and Danielson 1991, Chittaro 2004). One of the critical underlying assumptions of most Control-Impact assessments, and therefore of most existing assessments of MPAs, is that the available habitat within Control and Impact sites is similar. Careful Control site selection can reduce dissimilarities in available habitat between Control and Impact sites (and improve the validity of inferences). However, it is unrealistic to expect available habitat to be the same. García-Charton and Perez-Ruzafa (1999) have noted that few assessments of MPA effects have given quantitative attention to potentially confounding effects of environmental (e.g., habitat) heterogeneity, though the idea of such confounding effects is not new (e.g., Edgar and Barrett 1997; Chapman and Kramer 1999). A recent meta-analysis of the effects of MPAs (Halpern 2003) examined 89 separate empirical studies and found that mean densities for a wide range of species were significantly higher inside MPAs relative to reference areas. However, Halpern (2003) also acknowledged that habitat type and quality were not considered in his meta-analysis as many of the empirical studies reviewed typically did not report this information. Consequently, the degree to which unreported environmental heterogeneity may shape inferences regarding the effects of MPAs (e.g., are estimated effects more typically 'positive' because MPAs are often sited in the 'best' areas within a region?) remains uncertain.

In this chapter I address the potential biases in inferences that may arise from an implicit assumption of many researchers that chosen Impact and Control sites are 'roughly equivalent'. Specifically, I evaluate the effects of a collection of MPAs on Rarotonga (Cook Islands). Though I simultaneously collected data on many species as part of a wider study on the effects of MPAs, here I focus on a single species of reef fish to more clearly illustrate: 1) my approach, and 2) the potential biases in inferences that may arise as a result of differences in available habitat. My assessment framework is a simple Control-Impact design, supplemented with estimates of resource (in this case, substrate) use and resource availability relevant to my focal species. This supplemental information is used to adjust estimates of fish density, and facilitates empirical evaluation of potentially confounding effects of heterogeneous substrate between sites. However, this approach, which assumes substrate is simply a confounding variable that is not itself responding to protection, may mask MPA effects if available substrate is playing a role in determining differences in fish abundances between sites. Therefore, to address biases in inferences derived from my assessment framework, I compare my model with more commonly implemented analysis of covariance (ANCOVA) models with metrics of substrate availability as covariates, allowing the separation of the effects of protection from the effects of substrate availability. I suggest a combination of my approach and the more traditional use of ANCOVA models as an improved framework for future Control-Impact studies, particularly as BACIPS field assessments are often not feasible.

MATERIALS AND METHODS

Study system and species.

All work was conducted within the shallow lagoon system surrounding the island of Rarotonga, Cook Islands (latitude 21°12′S longitude 159°46′E, Figure 2.1). Lagoon depths reach a maximum of 3.5 metres on the windward side of the island, and 1.5 metres on the leeward side of the island, and habitat features within the lagoon system are spatially variable. The present lagoon system is divided into management zones (Figure 2.1) that are open to harvest, interspersed with management zones that are under some form of harvest control. Within these controlled areas, known as Ra'ui, some or all species may be protected from harvest, though the areas may be open to fishing from time to time (and compliance during periods of protection may be spatially and temporally variable)(See Chapter 1, Table 1.1). The Ra'ui, having no legal basis, rely on respect for traditional authority (Reid 2000). At the time of my surveys (autumn / winter 2005), there were 6 Ra'ui designated within the lagoon that were closed to the harvest of fish and invertebrates (Figure 2.1, see Chapter 1, Table 1.1).

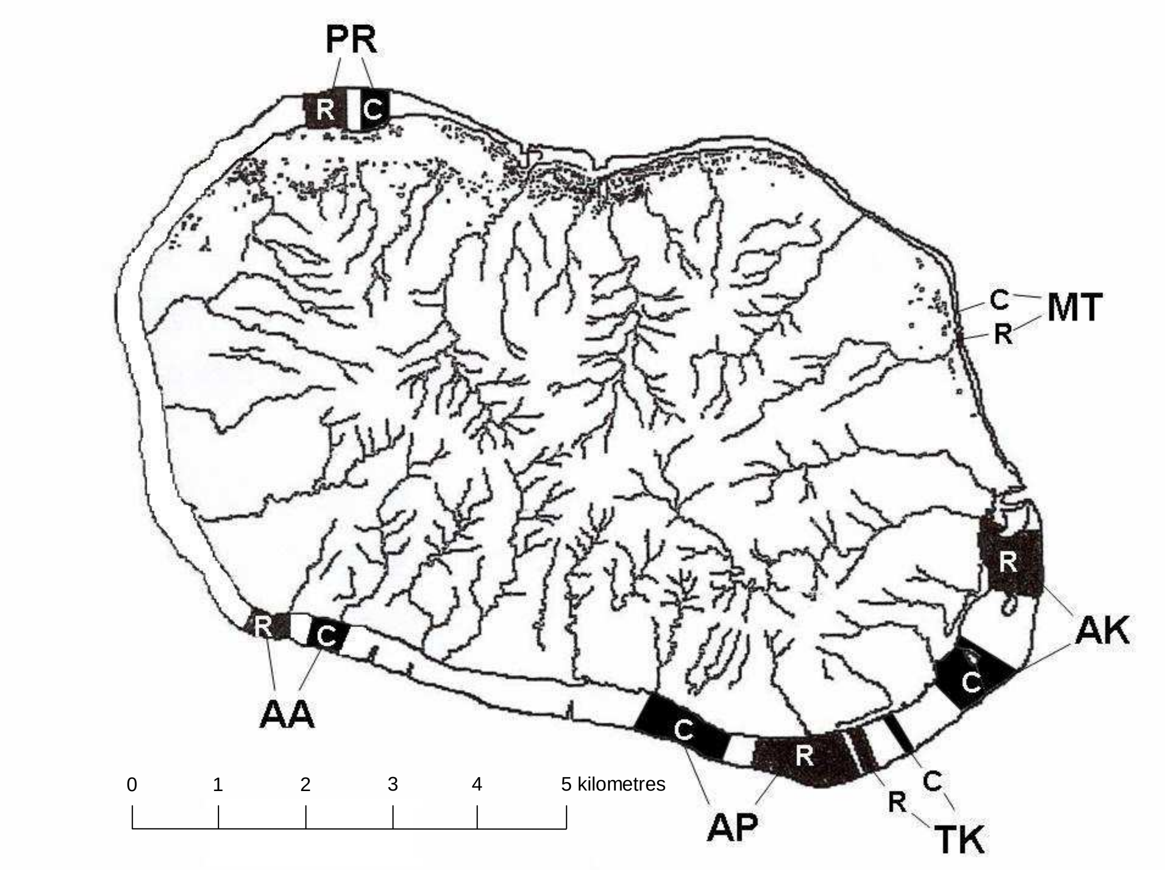


Figure 2.1. Map showing location of Ra'ui (R) [i.e., 'MPA' or 'Impact' sites] and corresponding non-Ra'ui [i.e., paired 'Control' (C)] sites around Rarotonga. Sites are coded as: AP = Akapuao, AA = Aroa, AK = Aroko, TK = Tikioki, MT = Matavera, PR = Parliament.

In this chapter I explore spatial patterns of abundance of the reef fish *Ctenochaetus striatus* in relation to Ra'ui and associated environmental features that may vary systematically among Ra'ui (= 'MPA' = 'Impact' site) and/or between Ra'ui and harvested (non-Ra'ui) areas (= 'Control' sites). *C. striatus* is found throughout the Indo-pacific region (excluding the Hawaiian, Marquesan and Easter Islands) (Randall 2005), is locally common in the lagoon surrounding Rarotonga (S. Miller, pers. obs.), and has been a favoured food fish, particularly in the southern group of the Cook Islands (McCormack 2007). *C. striatus* occurs in lagoons, on reef flats, and seaward reefs to depths over 30 metres, and can be found singly or in small to sometimes large, often mixed-species aggregations (Randall 2005). Using *C. striatus* as a focal species, (particularly as it occurred in abundances great enough to facilitate my statistical analyses), my overall aim is to evaluate the degree of concordance between estimates of reserve effects that either (1) ignore fine-scale habitat heterogeneity (implicit in most MPA assessments) or (2) attempt to statistically control for habitat heterogeneity relevant to the focal species.

Sampling regime

Field work was conducted between March and July 2005, with a total of 16 sites surveyed, including 6 Ra'ui paired with 6 'Control' sites (Figure 1). Paired Control sites were located at least 300m from Ra'ui boundaries and were selected and paired with Ra'ui based upon their proximity and qualitative similarities in depth, substrate composition and habitat complexity. All sites except for Matavera Ra'ui and its paired Control (due to an anomalously narrow lagoon) were spatially stratified into 'inner' and 'outer' strata, determined by the midpoint between the reef crest and shore for each site. Within each strata, 5 randomly located replicate transects (25m x 4m) were sampled once within all sites. In total, 150 transects were surveyed throughout the lagoon with all diurnally active fish, and numerous invertebrate species censused as part of a wider study investigating the responses of a suite of reef fish species and invertebrates to protection. I did not stratify my sampling 'by microhabitat' for each species because, like many MPA assessments, 1) habitat/resource requirements were not known a priori for most censused species and 2) such approaches are not practical for multi-species surveys (e.g., what may have been suitable habitat for one species, may not be suitable for other species).

I randomised spatial sampling through time to minimise potential biases arising from the sampling of sites/strata over a number of months and tidal cycles, as one of the objectives of the wider study was to investigate whether there were island-wide effects of Ra'ui. For each transect within strata I recorded: 1) counts of all *C. striatus*; 2) the substrate type upon which each individual *C. striatus* was initially observed, and; 3) fixed-point contact data (collected at 1m intervals in a uniform grid pattern within each transect) to estimate percent cover of substrate types over the area of the transect (125 points per transect – see below for description of substrates).

Ctenochaetus striatus is generally found in coral, rocky, pavement and rubble habitats (Lieske and Myers 2002). Based on this information (and information and observations of substrate use for other species examined as part of my wider study examining the effects of MPAs), I selected broad substrate categories based on prior observations in the field, and for ease of implementation during the surveys. Substrate was categorised as either: 1) **dead coral** (large upright limestone structures either cemented to substrate or else free from substrate but > ~60cm diameter, i.e., relatively immobile), 2) **live coral** (comprising genera: *Porites, Acropora, Pocillopora, Montastrea, Favia, Acanthastrea, Leptastrea, Hydnophora, Cyphastrea, Galaxea, Echinopora, Montipora, Millepora* species), (3) **sand**, 4) **pavement** (substrate that has been compressed and cemented into a conglomerate mass), 5) **rubble** (substrate ~0.5-60cm diameter but not cemented), 6) **turf algae** (filamentous algal species), and 7) all **other algae** (including *Anabaena torulosa, Halimeda*, *Turbinaria*, *Galaxaura*, and *Phorium spp*).

Environmental/ancillary information including depth, visibility, time and date of sampling, tide and lunar phase was also recorded. All sampling was conducted on snorkel in 0.5 - 3.5m water depths, between the hours of 9:00 and 16:00 to ensure diurnally active fish species were sampled (English *et al.* 1997).

Estimating effects of Ra'ui

Overview

My overall approach used a Control-Impact assessment framework (Osenberg and Schmitt 1996) to estimate the putative effects of individual Ra'ui in two separate ways: either with- or without adjustment for substrate availability. As some of the data did not meet the assumption of homogeneity of variance required by the Student's t-test (Quinn and Keough 2002), I used the Welch test to explore spatial variation in *C. striatus* densities (no./m^2 of bottom area, estimated from visual counts on replicate transects) between each Ra'ui and paired Control site.

I used permutational analysis of variance (PERMANOVA) (Anderson 2001; McArdle and Anderson 2001) to evaluate variation in substrate cover between each Ra'ui and paired Control site (i.e., 6 separate multivariate analyses were conducted). Arc-sine square-root transformed proportions of substrate cover comprised the set of independent variables, and my analyses tested the null hypothesis that substrate was homogenous in multivariate space for each set of paired sites. Substrate composition estimated from my fixed-point contacts was heterogeneous among sites (I suspect this is a common feature of most MPA assessments, though habitat heterogeneity is rarely quantified) (Figure 2.2).

Differences in available substrate between Ra'ui and Control sites, coupled with my observation that *C. striatus* did not appear to use all substrates equally, prompted me to quantify patterns of substrate use for *C. striatus* (detailed below), and then adjust estimates of 'available substrate' based upon species-specific substrate preferences. These adjusted estimates of available substrate facilitated adjustments of densities (on a *per 'available substrate basis'* as opposed to a *per m^2 benthos* measure). Variation in these 'preference-corrected' densities between each Ra'ui and paired Control were then analysed with Welch tests using the R statistical platform (R Development Core Team 2006). I directly tested for an overall effect of Ra'ui with a two-factor ANCOVA model with protection (i.e., Ra'ui or Control) and site as fixed factors and a substrate 'usability index' as the covariate. I then contrasted ANCOVA models for each Ra'ui / Control pair (protection as the fixed factor and substrate 'usability index' the covariate) to quantify sources of variation in *C. striatus* densities for each site and assess the utility of my adjusted densities.

Adjusting fish densities based upon substrate preference

I adjusted estimates of density by weighting substrate types by an index of resource selectivity, Manly's alpha (Manly 1974; Chesson 1978; 1983; Manly 1993). In this case, Manly's alpha provides a measure of preference for the different substrates *C. striatus* was observed on in the lagoon while accounting for natural variation in the availability of each substrate type at each site (Pledger *et al*. 2007).

For each of the seven substrate types (described above), Manly's alpha was calculated by taking the mean of separate Manly's alpha values calculated using the statistical platform, R (R Development Core Team 2006) across 16 sites around Rarotonga, including the 6 Ra'ui and Control site pairs (i.e., 12 sites). I calculated density two ways; one form yielded a simple density (number per area) (Equation 1), and the other yielded a 'preference-corrected' density in which the availabilities of substrates were weighted by their preference (Equation 2):

Equation 1)

$$D_t = N_t \Big/ \textstyle\sum_{i=1}^{k} s_{t,i} = N_t \Big/ A_t$$

and

Equation 2)

$$D_t = N_t \Big/ \textstyle\sum_{i=1}^{k} \alpha_i s_{t,i}$$

where N is the number of fish counted on a 100m^2 transect, t is the transect number, k is the number of substrate types (in this case, 7), s is the proportion of the transect represented by the substrate type, and α is Manly's alpha.

Evaluating Ra'ui effects using response ratios

I used logged response ratios (Hedges *et al*. 1999) generated from the average densities of *C. striatus* at each site [ln ($\text{density}_{\text{Ra'ui}}$ / $\text{density}_{\text{paired Control}}$)] to evaluate: (1) overall effects of Ra'ui on densities of *C. striatus* and, (2) concordance in estimates of effect sizes based upon simple versus substrate preference corrected densities. In my calculations, logged response ratios greater than zero indicate a positive response to protection; values of zero, or less than zero, indicate no response, or a negative response, respectively. 95% confidence intervals were calculated based on Hedges *et al.* (1999).

Direct test of overall Ra'ui effect

Using the statistical software package SPSS (SPSS 2008), I assessed the overall effect of Ra'ui using a two factor ANCOVA model (square-root transformed densities were the response variables; factors were level of protection i.e., Ra'ui or Control; and site) to evaluate variation in densities of *C. striatus* between Ra'ui and Control sites, with a substrate 'usability index' per transect (*S)* (Equation 3) as covariate:

Equation 3)

$$S_t = \sum_{i=1}^{k} \alpha_i s_{t,i}$$

where *k* is the number of substrate types (in this case, 7), *t* is the transect number, α is Manly's alpha, and *s* is the proportion of the transect represented by the substrate type.

Further, I treated each Ra'ui and Control pair as blocks in my ANCOVA analysis. My ANCOVA model explicitly tested the effect of Ra'ui, available substrate, and site (also evaluating the interaction between level of protection and site).

Contrasting simple and preference corrected density estimates with ANCOVA

I contrasted the logged response ratios of my simple density estimates and my 'preference-corrected' density estimates for each Ra'ui and Control pair with ANCOVA models for each site, again with 'substrate usability' index as the covariate. My aim was to assess the concordance of my simple and 'preference-corrected' density estimates at each site with those from my ANCOVA models, and to assess whether any statistical differences in densities between Ra'ui and Control were due to the effect of Ra'ui, or available substrate.

RESULTS

Substrate use by *Ctenochaetus striatus*

Substrate cover differed in 5 of the 6 Ra'ui / Control pairings (Figure 2). Only Aroa showed evidence of statistically indistinguishable habitat structure between the Ra'ui and its paired Control (Figure 2).

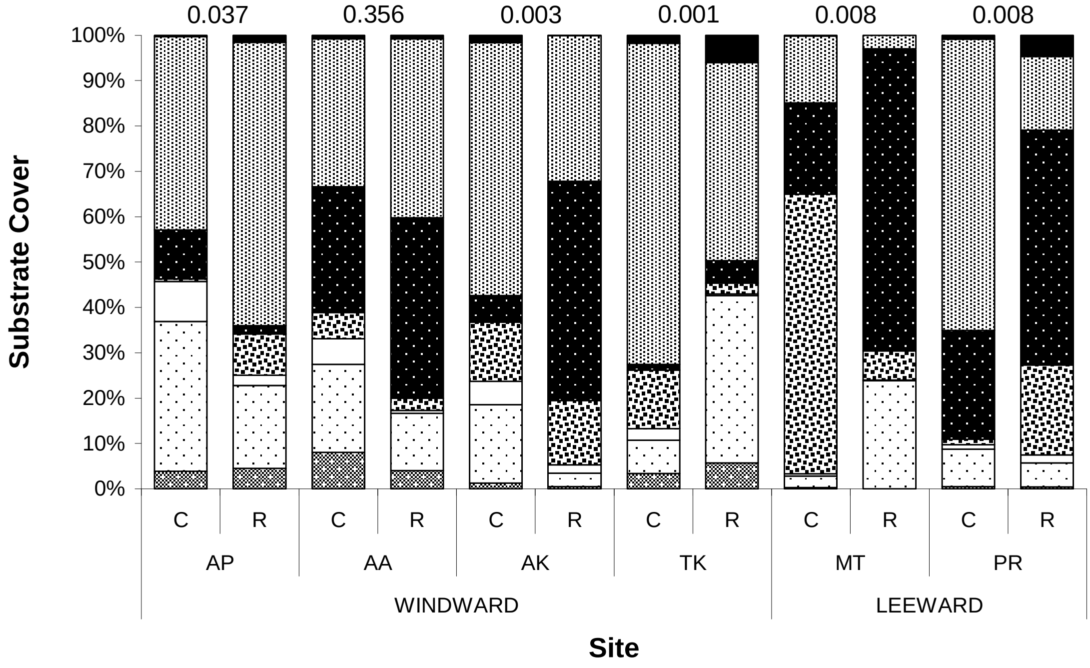


Figure 2.2. Cumulative percent cover of substrate per site by status (Ra'ui and Control). P-values at top of chart are results from a PerMANOVA of arc-sine square-root transformed proportion substrate cover for each Ra'ui and Control pair. AP = Akapuao, AA = Aroa, AK = Aroko, TK = Tikioki, MT = Matavera, PR = Parliament. TA ■ = turf algae, S ▒ = sand, R ▩ = rubble, P ▦ = pavement, OA □ = other algae, D ⬚ = dead coral, and C ▓ = live coral.

Manly's alpha values falling above or below a calculated value that is representative of random assortment (in this case, 0.143) reflect overuse (i.e., apparent preference) or under-use (i.e., apparent avoidance), respectively. Island-wide, *C. striatus* exhibited preference for dead coral and rubble substrates, and avoided live coral, other algae, pavement, sand, and turf algae (Figure 2.3).

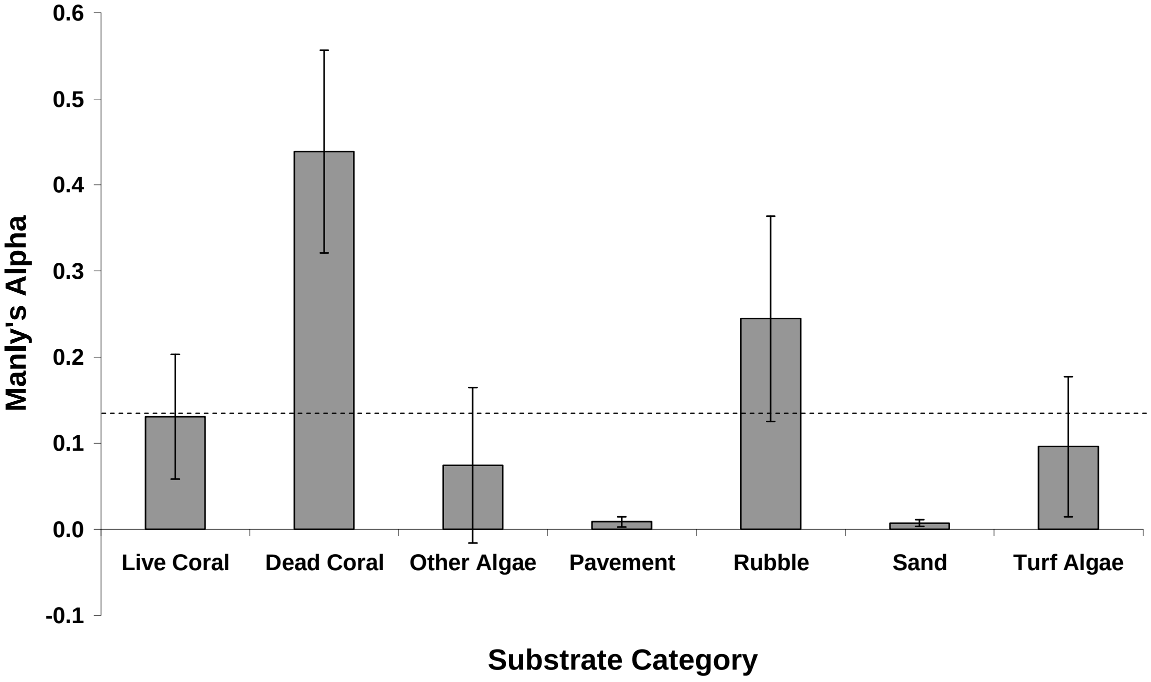


Figure 2.3. Lagoon-wide pattern of substrate use (error bars are 95% confidence intervals) by C. striatus across, evaluated for 7 substrates, as indicated by Manly's alpha. Dotted line depicts value of Manly's alpha consistent with random distribution; values above or below indicate overuse (preference) or under-use (avoidance) respectively.

Estimates of local Ra'ui effects

Fish densities

Simple mean densities of *C. striatus* within Ra'ui at Matavera and Parliament sites were significantly greater than densities estimated for paired Control regions by almost threefold (Figure 4A). For *C. striatus* densities estimated on a *per meter benthos* scale, all other Ra'ui and Control site pairings were statistically indistinguishable (Figure 4A). Based on adjusted density estimates, the estimated disparity between Parliament Ra'ui and its paired Control became more extreme (and remained significant based upon a Welch test). After adjusting for habitat heterogeneity, elevated densities inside the Matavera Ra'ui were no longer significantly different from the paired Control, and instead Akapuao Ra'ui appeared to have enhanced densities relative to its paired Control (Figure 4B). For Tikioki Ra'ui, adjusting densities based upon habitat heterogeneity modified my perceptions of relative abundance inside versus outside Ra'ui.

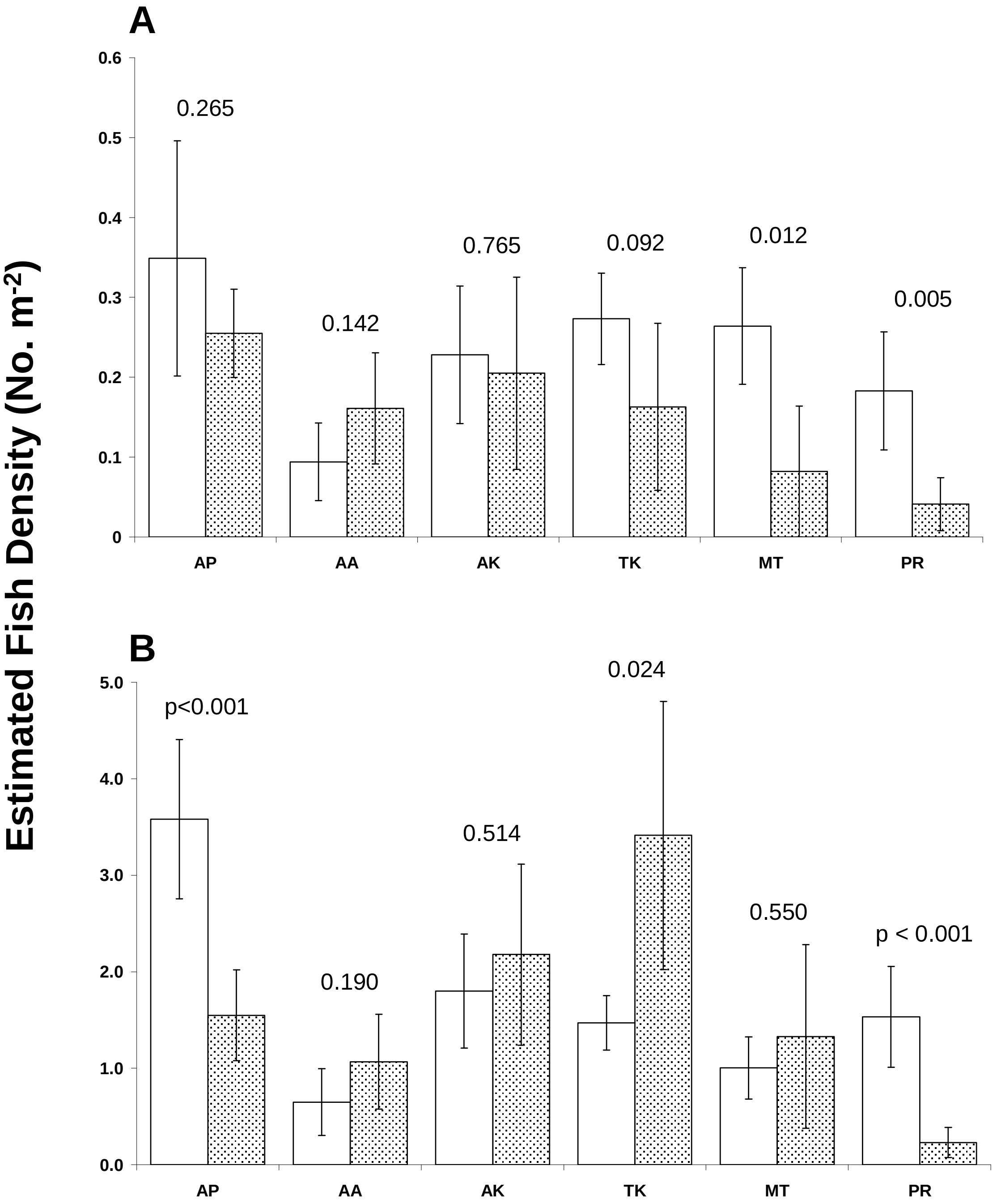


Figure 2.4. Densities of *C. striatus* pooled across strata for 6 Ra'ui and paired Control sites surveyed around Rarotonga. (error bars are 95% confidence intervals): A) per m^2 benthos, and B) per m^2 of 'useable' substrate. Results of Welch tests comparing densities between each Ra'ui and paired Control site are reported as *p-values* above each site. Note: scales differ between A and B. AP = Akapuao, AA = Aroa, AK = Aroko, TK = Tikioki, MT = Matavera, PR = Parliament. ☐ = Ra'ui, ⬚ = Control.

Direct test of an overall Ra'ui effect

My two-factor ANCOVA model, with level of protection and site as fixed factors, and 'useable substrate' index the covariate, indicated that both site and substrate significantly contributed to variation in *C. striatus* densities across all Ra'ui (Table 2.1). There was also a significant interaction between the level of protection and site (Table 2.1).

Table 2.1. Two factor analysis of covariance (factors = protection and site) evaluating densities of *C. striatus* across all Ra'ui and Control sites, with index of 'usable substrate' as covariate.

Treatment	df	MS	F-ratio	p	Estimated Marginal Mean	
					Ra'ui	Control
Full model	12	0.208	11.139	p < 0.0001	0.408	0.367
Protection	1	0.037	1.985	0.162		
Site	5	0.195	10.465	p < 0.0001		
Substrate	1	0.935	50.053	p < 0.0001		
Protection X Site	5	0.065	3.489	0.006		
Error	97					

Response to protection – simple data versus substrate adjusted data

In the context of a Control-Impact framework, inferred responses of *C. striatus* to protection are given as logged response ratios (Figure 2.5). This graphical analysis suggests that *C. striatus* exhibited a heterogeneous response to protection across all Ra'ui sites, based upon either the simple density estimates or 'preference-corrected' estimates. Basing inferences on simple density estimates, Matavera and Parliament Ra'ui appeared to have a positive effect on *C. striatus* density; the inferred effects of all other Ra'ui were equivocal (Figure 2.5).

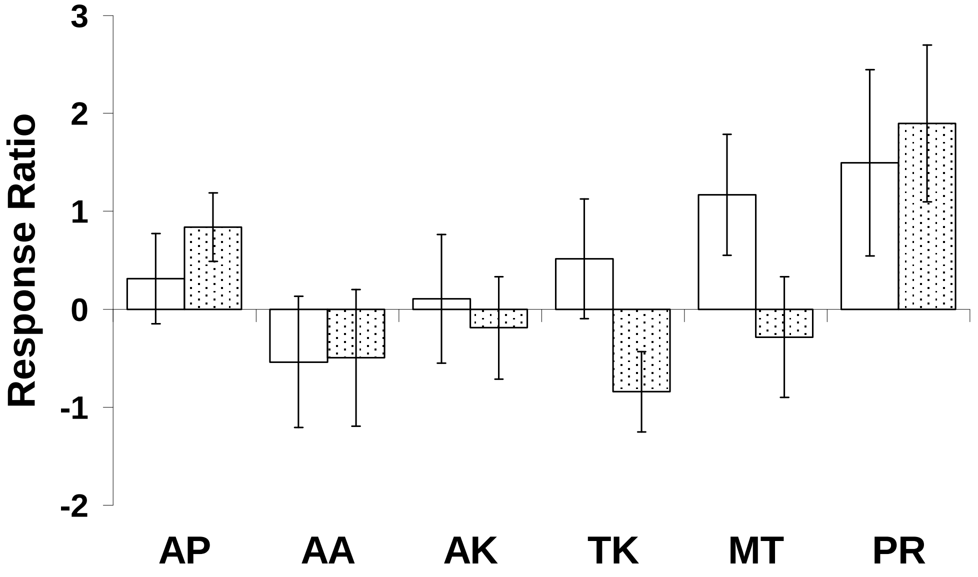


Figure 2.5. Logged response ratios [Ln ($\text{density}_{\text{Ra'ui}}$ / $\text{density}_{\text{Control}}$)] as an estimate of Ra'ui effects, calculated for simple densities and 'preference-corrected' densities. Error bars are bootstrapped 95% confidence intervals. AP = Akapuao, AA = Aroa, AK = Aroko, TK = Tikioki, MT = Matavera, PR = Parliament. ☐ = simple densities, ⬚ = 'preference-corrected' densities

Basing inferences upon 'preference-corrected' densities, *C. striatus* appeared to respond favorably to protection from harvest at Akapuao and Parliament, and negatively to protection from harvest at Tikioki (Figure 2.5). In several cases (e.g., Tikioki and Matavera), adjusting for substrate heterogeneity qualitatively modified inferences of MPA effectiveness (Figure 2.5).

Variation in fish densities

ANCOVA models to quantify the sources of variation in *C. striatus* densities between paired Ra'ui and Control sites suggested there were significant differences between Ra'ui and Control *C. striatus* densities at 4 of the 6 Ra'ui sites (Table 2.2). However, Ra'ui accounted for this difference at only one site, Parliament. For Akapuao, Aroko, Parliament, Matavera, and Tikioki, the total percentage of preferred substrate accounted for a significant amount of variation in *C. striatus* densities between paired Ra'ui and Control sites (Table 2.2). Further, there was an interaction between protection and substrate at Akapuao and Tikioki Ra'ui. There was a significant interaction between Ra'ui (level of protection) and the total percentage of preferred substrate at Akapuao, Matavera, and Tikioki (Table 2.2).

Estimated marginal mean *C. striatus* densities were calculated from my ANCOVA model in SPSS (SPSS 2008) (Table 2.2). Estimated marginal mean *C. striatus* densities were significantly greater at Akapuao and Parliament Ra'ui sites, and significantly lower at Aroko and Tikioki Ra'ui sites than corresponding Control sites (Table 2.2). There were no significant differences in *C. striatus* estimated marginal mean densities at Aroa or Matavera Ra'ui and their corresponding Control sites (Table 2.2). The direction of my simple *C. striatus* density responses were concordant with the direction of paired Ra'ui / Control estimates from my ANCOVA model at only two of the six sites, Aroa and Parliament (Table 2.2, Figure 2.4). However, the direction of my adjusted density estimates were concordant with the direction of my ANCOVA model estimated densities at five of the six sites (Table 2.2, Figure 2.4).

Table 2.2. Analysis of covariance evaluating densities of *C. striatus* between separate Ra'ui and corresponding Control sites, with index of 'usable substrate' as covariate. Given are separate analyses for each Ra'ui/Control site pairing. Estimated marginal means of *C. striatus* densities (with covariates held at their overall mean value) are included in the table.

SITE	**Treatment**	**df**	**MS**	**F-ratio**	**p**	**Estimated Marginal Mean**	
						Ra'ui	**Control**
AKAPUAO	Full model	3	0.128	11.088	p<0.001	0.664	0.464
	Protection	1	0.005	0.408	0.532		
	Substrate	1	0.297	25.734	p<0.001		
	Protection X Substrate	1	0.093	8.046	0.012		
	Error	16	0.012				
AROA	Full model	3	0.022	0.76	0.533	0.263	0.373
	Protection	1	0.008	0.291	0.597		
	Substrate	1	0.003	0.114	0.74		
	Protection X Substrate	1	0.00001	0	0.983		
	Error	16	0.029				
AROKO	Full model	3	0.183	12.703	p<0.001	0.412	0.447
	Protection	1	0.009	0.616	0.444		
	Substrate	1	0.539	37.364	p<0.001		
	Protection X Substrate	1	0.025	1.726	0.207		
	Error	16	0.014				
TIKIOKI	Full Model	3	0.117	11.571	p<0.001	0.461	0.579
	Protection	1	0.017	1.646	0.218		
	Substrate	1	0.191	18.941	p<0.001		
	Protection X Substrate	1	0.069	6.804	0.019		
	Error	16	0.01				
MATAVERA	Full model	3	0.064	2.6	0.565	0.742	0.231
	Protection	1	0.02	1.967	0.121		
	Substrate	1	0.008	0.824	0.049		
	Protection X Substrate	1	0.007	0.312	0.044		
	Error	6	0.025	0.277			
PARLIAMENT	Full model	3	0.205	20.827	p<0.001	0.385	0.178
	Protection	1	0.153	15.567	0.001		
	Substrate	1	0.222	22.58	p<0.001		
	Protection X Substrate	1	0.025	2.491	0.134		
	Error	16	0.01				

DISCUSSION

Adequate assessments of interventions such as MPAs are vital in order to understand MPA effects and ensure MPAs meet their conservation goals. In this study I demonstrate the effects of incorporating substrate availability into MPA assessments. Ignoring putative effects of substrate availability and using a standard Control-Impact assessment framework (the most common form of MPA assessment), I inferred a varying response of *C. striatus* to protection across the 6 censused Ra'ui. When substrate availability was incorporated into my analyses, perceptions (i.e., inferences derived from a set of Control-Impact assessments) were altered. My two-factor ANCOVA model assessing an overall Ra'ui effect also suggested that *C. striatus* had a variable response to protection across Ra'ui. I suggest that my framework for adjusting densities as a function of the relative abundance of, and preferences for, substrate types may provide more meaningful estimates of density in a set of observations where substrates (and preferences) may be heterogeneous. At any rate, my approach facilitates a quantitative comparison of effect sizes (i.e., inferred effects of MPAs) with and without adjustment for substrate availability (e.g., Figure 5). Further, my ANCOVA models of *C. striatus* densities at each site were concordant with my 'preference-corrected' model for 5 of the 6 Ra'ui / Control paired sites, giving support to my adjusting densities for 'useable' substrate.

ANCOVA models indicated that the majority of *C. striatus* densities at each site were influenced by substrate availability. Consequently, it is likely the lack of significant differences in *C. striatus* 'preference corrected' densities (see Figure 2.4) between Ra'ui and corresponding Controls at Aroa, Aroko, and Matavera were due to each Ra'ui having a similar index of 'usable substrate' (S) to its paired Control, whereas S was higher at Ra'ui for Akapuao and Parliament, and lower at Tikioki, than its paired Control site. Subsequent Welch t-tests using the R statistical platform (R Development Core Team) of the respective null (and alternative) hypotheses (i.e., $H_0 = S_{Ra'ui} = S_{Control}$, $H_A = S_{Ra'ui} \neq S_{Control}$ (Aroa, Aroko, and

Matavera), $H_0 = S_{Ra'ui} = S_{Control}$, $H_A = S_{Ra'ui} < S_{Control}$ (Tikioki), and $H_0 = S_{Ra'ui} = S_{Control}$, $H_A = S_{Ra'ui} > S_{Control}$ (Akapuao and Parliament) were accepted for Aroa (t = -0.265, df = 17.04, p = 0.794), Aroko (t = 0.929, df = 17.68, p = 0.366), and Parliament (t = 5.839, df = 17.64, p = 0.794) and rejected for Matavera (t = 11.316, df = 6.93, p ≤ 0.001), Tikioki (t = 5.839, df = 17.64, p ≤ 0.001), and Akapuao (t = -2.560, df = 17.93, p = 0.010) confirming my suppositions regarding 'usable substrate' at 4 of the 6 sites. In contrast, Parliament did not have greater 'useable substrate' at Ra'ui sites, indicating that Ra'ui (or some other factor that I failed to quantify e.g., habitat rugosity) contributed to greater *C. striatus* densities at the Parliament Ra'ui than at its corresponding Control. This result also agreed with the ANCOVA model for Parliament (Table 2.2) where protection accounted for a significant amount of variation in *C. striatus* densities between Ra'ui and Control sites.

Response ratios enabled the magnitude of effect for both simple and adjusted density estimates to be quantified. Further, ANCOVAs with substrate as covariates indicated whether protection or substrate contributed to variation in fish densities between paired Ra'ui and Control sites. Increasingly, alternatives to null-hypothesis significance testing such as effect size statistics are being advocated in the biological sciences (Nakagawa and Cuthill 2007; Stephens *et al* 2007). The use of effect sizes (e.g., response ratios) provides more biologically meaningful information relative to standard null hypothesis significance tests, because these approaches give information on both the magnitude of the effect, and the precision of the effect size estimate (Nakagawa and Cuthill 2007). Further, estimates of effect size with confidence intervals can provide clear and informative conclusions that can become the basis for decision-making (Stewart-Oaten 1996), and enable the quantification of the response to a restoration activity such as the implementation of an MPA (Osenberg *et al*. 2006). Although response ratios generated from my preference corrected densities don't provide specific information regarding the sources of variation contributing to differences in fish densities between sites, this information could still be used as a baseline for future work with increases or decreases in effect size as indications of recovery or decline, respectively. Further, the concurrent use of ANCOVA models can partition sources of variation to ascertain, for example, whether differences between sites are due to protection or substrate availability or a combination of these two factors. Together, my two approaches increase biological inferences that can be gained from MPA assessments.

That available substrate appears to affect densities of organisms is not a novel finding. It is generally acknowledged that habitat availability is a factor contributing to the abundance of many species, including fish (Bell and Galzin 1984, Pulliam and Danielson 1991, Chittaro 2004). In contrast, few assessments of MPAs (reviewed in Halpern 2003; Osenberg *et al*. 2006) consider (in any quantitative form) the potentially confounding effects of environmental heterogeneity in their design, analysis, or interpretation.

Though confounding effects of spatio-temporal variation are perhaps best dealt with in more sophisticated assessment designs (e.g., BACIPS, *sensu* Stewart-Oaten *et al*. 1986), there is often little opportunity to collect required 'Before' data (e.g., Mosquera *et al*. 2000; Parnell *et al*. 2005; Floeter *et al*. 2006). Consequently, many previous assessments of MPA effectiveness have been simple Control-Impact studies, or a variation on this type of study (Osenberg *et al*. 2006). Control-Impact studies do not typically incorporate habitat heterogeneity into assessment designs, though some workers have acknowledged this as a limitation in their work (e.g., Parnell *et al.* 2005; Floeter *et al.* 2006). Several previous studies have attempted to account for environmental variation by incorporating information regarding habitat or environmental heterogeneity into their analyses (Buxton and Smale 1989; Tuya *et al*. 2000; McClanahan and Arthur 2001; Friedlander *et al.* 2003; Westera *et al.* 2003; Willis and Anderson 2003; Evans and Russ 2004; Friedlander *et al.* 2007), usually via analysis of covariance (ANCOVA) with environmental variables as covariates, or regression analysis with environmental variables being a single, or one of many, predictor variables.

Control-Impact studies are sometimes replicated through time after establishment of an MPA (e.g., Russ and Alcala 1996; Russ and Alcala 1998a, b; Begg *et al.* 2005; Micheli *et al.* 2005; Tuya *et al*. 2006). However, the coupling of temporal and spatial variability (García-Charton and Pérez Ruzafa 1999), suggests that, as with one-off Control-Impact studies, temporally replicated Control-Impact studies are still prone to confounding by natural spatial variability between the Control and Impact sites, independent of the intervention (Osenberg and Schmitt 1996).

BACIPS sampling designs, or sampling designs with some elements of BACIPS, have been used more recently by some workers to separate the effects of MPAs from natural temporal and spatial heterogeneity (e.g., Nardi *et al.* 2004; Lincoln-Smith *et al*. 2006; Shears *et al.* 2006; McClanahan *et al.* 2007; Samoilys *et al.* 2007). BACIPS is currently among the most rigorous survey protocols that could be used to assess MPA effectiveness (Lincoln-Smith *et al*. 2006; see Osenberg *et al*. 2006 for a discussion and modification of this design pertinent to MPAs). However, this type of survey design is often not feasible (e.g., because assessments are rarely planned and implemented in advance of MPA legislation and/or enforcement; reviewed in Osenberg *et al*. 2006).

The approach I have used to assess the effects of MPAs is novel in that it incorporates an index of resource selectivity (Manly’s alpha) into a Control-Impact assessment framework, as a weighting factor to account for environmental variation between sites. Alternately, I also demonstrated the index of Manly’s alpha can be used to determine ‘preferred’ habitats for an organism, and a substrate ‘usability index’ can then be used as a covariate in an ANCOVA model. There are a number of indices used to estimate selection of a resource by an organism (Manly *et al*. 2002). Generally, resource selection functions have been used to look at food and habitat selection (Popham 1944; Neu *et al*. 1974; Light and Jones 1997; Dudas *et al*. 2005; Meyer *et al*. 2007). In the context of marine reserves, La Mesa *et al*. (2006) used a modification of Ivlev’s (1961) electivity index to assess the preference of cryptobenthic fish fauna in a Mediterranean marine reserve. As far as I am aware, no-one has yet used resource selection indices to incorporate available habitat into assessments of MPA effects. Strong habitat associations are clear and important features of many reef fish and invertebrate assemblages (e.g., Chittaro 2004). When using assessment frameworks that are sensitive to natural spatial variation in habitat features (e.g., Control-Impact studies covering a broad suite of species), I suggest that an explicit, quantitative incorporation of habitat heterogeneity into analyses facilitates a more robust and defensible set of inferences.

When beneficial effects of MPAs are inferred from Control-Impact studies, an alternative interpretation is that the observations reflect a pre-existing difference between an MPA and Control site (e.g., because MPAs may typically be sited in the 'best' available locations within a region; Osenberg *et al*. 2006). My inability to sample prior to the Ra'ui being implemented means I was unable to assess whether available substrate had changed due to protection (with subsequent indirect effects on faunal abundances). However, when I evaluated a set of Control-Impact studies while ignoring substrate heterogeneity, ~83% of MPAs (i.e., 5 of 6 Ra'ui) showed some evidence of being 'effective' for *C. striatus* (i.e., positive response ratios in Figure 2.5). When I adjusted densities by preferred substrate availability, only ~33% of MPAs (2 of 6 Ra'ui) showed any evidence of effectiveness. One interpretation of this pattern is that some Ra'ui on Rarotonga may be sited in particularly good sites with respect to *C. striatus*, and my approach effectively controlled for this underlying variation in substrate availability. Further, analysis using ANCOVA demonstrated this may be the case for 4 out of 6 of the Ra'ui sites surveyed i.e., substrate availability accounted for variation in fish densities between sites, not Ra'ui.

I note that my set of Control-Impact studies suggest that *C. striatus* on Rarotonga appear to exhibit heterogeneous responses to protection regardless of my treatment of habitat heterogeneity (Figure 2.5). This may be attributable to spatial variation in: 1) compliance and/or fishing history associated with each

MPA (some Ra'ui on Rarotonga are occasionally open to harvest) and the degree to which *C. striatus* is harvested, 2) demographic rates of *C. striatus* (e.g., recruitment and/or natural mortality), and/or 3) higher order ecological interactions (e.g., trophic cascades impinging upon *C. striatus* that vary among Ra'ui, depending upon the structure of the local community). Additionally, some component of my observed responses may still be prone to underlying spatial variation in environmental features that I did not quantify between each Ra'ui and its paired Control site, with the unquantified environmental components (e.g., habitat complexity, rugosity) 'swamping' the quantified substrate-related effects.

CONCLUSIONS

My study empirically demonstrates how environmental heterogeneity can impinge upon interpretations of MPA assessments. Many reef organisms exhibit strong habitat preferences, and marked spatial variation in habitat features characterizes many reefs. Where Control-Impact assessments are subject to bias (e.g., protected areas are sited in areas of 'better habitat' than corresponding control sites), bias can be reduced using my framework. Hence, I advocate incorporation of substrate heterogeneity into assessment designs that are confounded by natural spatial variation (e.g., Control-Impact studies) whenever more robust assessments (e.g., BACIPS) are not feasible. Further, my framework may even improve the power of BACIPS assessments, through accounting for variation attributable to putative substrate differences between sites. My framework allows quantification of effect sizes between different Ra'ui, and coupled with an ANCOVA model, some indication of sources of variation.

CHAPTER 3: Fish, invertebrate, and functional group responses to Ra'ui using a novel assessment framework for marine protected areas

ABSTRACT

Marine protected areas (MPAs) are generally expected to increase the abundance, size, diversity and biomass of organisms within their boundaries. However, our ability to generalise these effects across species and / or locations is limited by uncertainties associated with existing assessment methodologies. Most MPA assessments are Control – Impact studies, but an unavoidable limitation of such studies is uncontrolled variation between the Control site and the Impact site. Hence, spatial variation in critical habitat features (e.g., abundance or structure) that shapes distributions of organisms can confound any reserve effect. I chose to address this problem within the framework of a simple control-impact assessment framework by weighting densities of censused organisms by 'preferred substrate'. Here, I used this novel analytical approach (described in Chapter 2) to explore the effects of Ra'ui across a broad range of species (fish and invertebrates) and functional groups found within the lagoon of Rarotonga. I applied meta-analytical methods to assess whether there was an overall island-wide effect of Ra'ui for any of the species or functional groups examined and found no overall Ra'ui effect. However, in quantifing sources of variation in fish, invertebrate, and functional group densities with a blocked two-factor analysis of covariance, there was an island-wide effect of Ra'ui for some species. Results indicated that responses to protection were highly variable for species and functional groups both within and across Ra'ui. However, some analyses suggest that predator densities are enhanced in some of the Ra'ui. This Chapter illustrates how

apparent responses to protection (i.e., MPA effects, as estimated by Control-Impact studies) can vary even when careful attempts are made to control for habitat heterogeneity (one source of variation that potentially confounds estimates of MPA effects).

INTRODUCTION

Fishing is now one of the main anthropogenic activities affecting life in the oceans (Edgar *et al.* 2005). In attempts to mitigate human impacts (primarily fishing) on marine ecosystems (Roberts and Polunin 1991, 1992, Sumaila *et al.* 2000, Roberts *et al.* 2001), marine protected areas (MPAs) are increasingly being advocated and implemented around the world. MPAs are an intervention used to modify human fishing behaviour through restrictions on, or complete exclusions of fishing (see Agardy *et al.* 2003 for discussion on the definition of MPAs). MPAs are rapidly becoming conventional tools for the conservation of biodiversity (Agardy *et al.* 2003) and the management of fisheries (Boersma and Parrish 1999), with a general expectation that MPAs will have direct effects that include increased numbers, size, biomass, and diversity of organisms within their bounds (Roberts and Polunin 1992, McClanahan 1994, Roberts 1995b, Jennings *et al.* 1996b, Russ and Alcala 1996, Wantiez *et al.* 1997, McClanahan *et al.* 1999, Tuya *et al.* 2000, McClanahan and Arthur 2001, Claudet *et al.* 2006).

Evidence from several recent reviews of research on MPAs suggests that no-take MPAs result in greater overall fish density, size, biomass and diversity relative to reference areas (Roberts and Polunin 1993, Francour *et al.* 2001, Halpern and Warner 2002, Russ 2002, Halpern 2003). The abundance and size of larger carnivores and heavily fished species has been shown to be greater inside protected areas than in fished areas (Roberts and Polunin 1993, Rowley 1994, Francour *et al*. 2001). However, there is also evidence of differential responses to protection of different trophic groups (Palumbi 2004), community-wide effects of protection (Roberts and Polunin 1991), and trophic cascades occurring in fished areas relative to protected areas (Pinnegar *et al.* 2000, Francour *et al.* 2001).

Recent meta-analyses of the effects of MPAs have concluded that fish abundance often varies between MPAs and reference sites. For example, Mosquera *et al.* (2000) found the overall abundance of fish inside reserves to be significantly (3.7 times) greater than outside; similarly, Côté *et al.* (2001) noted a non-significant (25%) increase in overall fish abundance inside versus outside MPAs. However, in some analyses non-target fish species appear to have similar abundances in fished and protected areas (Mosquera *et al.* 2000, Côté *et al.* 2001), and in some cases, abundance may be lower inside MPAs. It is clear that putative effects of MPAs vary (though most studies cannot strongly attribute observed variation to MPA effects), and some authors have suggested that such variability may result from higher-order effects that may, for example, include indirect effects of protection occurring via induced changes in predatory and/or competitive interactions (Micheli *et al.* 2005). Nonetheless, many published meta-analyses concur that (1) abundances of species targeted by fishing often increase inside reserves relative to reference areas (Mosquera *et al.* 2000, Côté *et al.* 2001, Micheli *et al.* 2005), and (2) top trophic levels often comprise a greater proportion of total fish biomass in protected areas (Micheli *et al.* 2005).

Meta-analyses have been successfully applied to ecological questions (Hedges *et al.* 1999, Osenberg *et al.* 1999). The analytical framework provides an excellent means of integrating and collectively analysing results from separate studies (Hedges and Olkin 1985), and the approach has recently been used to evaluate generalised effects of MPAs (Mosquera *et al.* 2000, Côté *et al.* 2001, Micheli *et al.* 2004, Ojeda-Martinez *et al.* 2007). Whereas standard reviews conventionally use significance values (e.g., p-values) to 'vote-count' (Hedges and Olkin 1985), meta-analysis requires an estimation of 'effect size' for each of the separate studies incorporated in the meta-analysis. The effect size from each individual study is then subject to further analysis (Osenberg *et al.*. 1999). The use of effect sizes provides biologically more meaningful information than that from standard null hypothesis significance tests which tend to form the basis of most reviews, because estimates of effect size give information on both the magnitude of the effect, and the precision of the effect size estimate (Nakagawa and Cuthill 2007). However, to date, no meta-analyses of the effects of MPAs have incorporated habitat.

Variability in estimates of MPA effects are not unexpected, as there are many processes that may act to obscure and/or confound MPA effects. Many ecological processes (e.g. disturbance, competition, facilitation and predation) can affect demographic rates (e.g., mortality, growth, maturation and fecundity) to shape patterns of abundance and community structure of marine organisms (Jones *et al.* 1991). For example, sampling artefacts and associated difficulties with acquiring representative samples (Samoilys and Carlos 2000), environmental heterogeneity (reviewed in García-Charton and Perez Ruzafa 1999), variable recruitment (Russ and Alcala 1998a), and indirect effects such as trophic interactions (Shears and Babcock 2002, Dulvy *et al.* 2004a) can all mask and/or confound MPA effects.

In Chapter 2 I demonstrated how MPA effects can be confounded by differences in habitat between Ra'ui and Control sites, and developed a novel approach to address incorporating habitat into the assessment of MPA effects. Here, I adopt the approach that I developed in Chapter 2 and apply it to a broad range of species and functional groups. My objectives were to investigate the effects of Ra'ui across a range of fish and invertebrate species, and fish functional groups, using the statistical approach that I developed in Chapter 2. This approach modifies a simple Control-Impact assessment framework, and addresses some of the limitations that may affect many MPA assessments. Specifically, while controlling for natural variation in 'available substrate', I address the following questions: (1) Do Ra'ui effects vary among sites and across species and functional groups? (2) Using meta-analysis, is there an island-wide Ra'ui effect across species and functional groups? Further, using a blocked two-factor ANCOVA, I assess whether substrate availability or protection, or a combination of protection and substrate availability drive any statistical differences in island-wide densities between Ra'ui and Control sites. Detailed hypotheses are outlined in Box 3.1.

Box 3.1 Hypotheses (when statistically controlling for habitat differences)

1. Densities of harvested fish species (for example, Mullidae (goatfish), *Naso* species (unicornfish), Scaridae (parrotfish), Siganidae (rabbitfish), and Serranidae (grouper)) will be greater in Ra'ui than corresponding Control sites.
2. Densities of harvested invertebrate species such as Echinometridae and Diadematidae (urchins), Tridacnidae (giant clams), *Dendropoma maxima* (wormsnail), *Trochus niloticus* and *Turbo setosus* will be greater in Ra'ui than Control sites.
3. Responses to protection exhibited by invertebrates will be stronger due to the sedentary / sessile nature of a many invertebrate species relative to many reef fish.
4. Reef crest invertebrates will exhibit a stronger response than either lagoon fish or lagoon invertebrates, as reef crest invertebrates are more readily visible and accessible to fishers, especially at low tide when the reef crest is exposed.
5. At the functional group level, the density of carnivores (which tend to be larger, slower growing, often fished, species) will be greater in Ra'ui than Control sites.
6. Densities of prey species will be lower or the same in Ra'ui relative to corresponding control sites due to predator-prey interactions arising from enhanced predator abundances in Ra'ui (see hypothesis 5 above).
7. For each species or functional group, there will be a general Ra'ui effect across all sites

MATERIALS AND METHODS

Study System and Sampling Regime

Research was conducted within the shallow lagoon system surrounding the island of Rarotonga, Cook Islands (21°12′ S, 159°46′ W). A detailed description of the study system and sampling programme conducted in the lagoon between March and July 2005 can be found in Chapter 2.

In addition to the lagoon sampling described previously, I surveyed invertebrates at additional locations on the reef crest (conducted at low tide) for two pairs of Ra'ui / Control sites. Within each lagoon strata, and at each sampled reef crest location, five randomly positioned replicate transects (25m x 4m) were surveyed once within all sites. In total, I surveyed 110 transects throughout the lagoon and 20 transects on the reef crest.

Data were recorded for all diurnally active fish species (136 species in total) within the lagoon and 18 invertebrate species on the reef crest and in the lagoon. Each species was counted and the substrate type upon which each individual was initially observed was recorded. For each transect, I used fixed-point contact surveys (collected at 1m intervals in a uniform grid pattern) to estimate percent cover of substrate types (125 points per transect). Detailed descriptions of the seven substrate types discriminated and characterised during lagoon surveys can be found in Chapter 2. Percent cover and substrate use was estimated for only six substrate types present at the reef crest (i.e., turf algae did not occur in any of the censused transects and was thus excluded) (Appendix A, Figure 1).

All lagoon sampling was conducted on snorkel in water 0.5 - 3.5m water deep, between the hours of 9:00 and 16:00 to ensure diurnally active fish species were sampled (English *et al.* 1997). Reef crest sampling was conducted at low tide, on foot, during daylight hours.

Data analysis

Estimating robust effect sizes for Control-Impact derived data

In Chapter 2, the effects of a collection of MPAs were estimated for one species of reef fish (*Ctenochaetus striatus*), and inferences drawn from a standard analytical approach were evaluated against those of a novel approach (in concert with a more traditional ANCOVA approach) that attempted to control for the confounding effects of substrate heterogeneity (see Chapter 2 for details). The novel approach developed and evaluated in Chapter 2, and also used here, integrates a standard Control-Impact study design with an index of resource selectivity (Manly's alpha). I use Manly's alpha to re-weight densities obtained from standard censuses to effectively account for spatial variation in the availability of each substrate type among sites (Chesson 1983). I then use response ratios (Hedges *et al.* 1999) as a metric of effect size for treatments (e.g., intervention = Ra'ui) effect size, calculated from weighted densities to estimate an effect of Ra'ui on focal organisms (Chapter 2, see Halpern 2003, Cole *et al.* 2007, Samoilys *et al.* 2007 for further examples of the use of response ratios in ecological studies).

Quantification of Ra'ui Effects Using Log Response Ratios

To evaluate the effect of Ra'ui on densities of individual fish species, invertebrate species, and fish functional groups, logged response ratios [ln ($\text{density}_{\text{Ra'ui}}$ / $\text{density}_{\text{paired Control}}$)], a common measure of experimental effect (Hedges *et al.* 1999), were calculated at each site for substrate-adjusted densities. Log response ratios greater than zero indicate a positive response to protection; values of zero, or less than zero, indicate no response, or a negative response, respectively. 95% bootstrapped confidence intervals were calculated based on Hedges *et al.* (1999).

Island-wide assessment of Ra'ui effects

a) Applying a Meta-analysis to Response Ratios

Meta-analytical techniques, which require estimates of effect size (Hedges and Olkin 1985), were applied to the response ratios on fully protected Ra'ui sites. Using a random effects model, the average effect size across all sites (the weighted mean of the log response ratios) (Hedges *et al.* 1999) was calculated in Microsoft Excel to assess whether there was an overall Ra'ui effect across sites for any of the fish and invertebrate species, and functional groups, and whether general inferences could be made regarding island-wide Ra'ui effects for a species or functional group. Parametric confidence intervals were calculated based on Hedges *et al.* 1999.

Meta-analysis was chosen in conjunction with null hypothesis significance tests (NHST) because although NHSTs provide a measure of statistical significance, this is not necessarily correlated with biological significance (Fernandez-Duque 1997). Meta-analysis provides an estimate of effect size while methods for combining p-values from NHST do not give any indication of the magnitude of effects, and NHST ignores small effect sizes (i.e., where often in ecological studies the sample size is too small to give a 'statistically significant' result) (Fernandez-Duque 1997). Meta-analysis enables the combination and synthesis of individual studies or 'experiments' with varying sample sizes (Fernandez-Duque and Valeggia 1994), and allows a combined estimate of 'response to Ra'ui' to be generated across all sites which are weighted depending on the precision of the estimate. Sites where measurements are more precise receive greater weight while less precise estimates receive less weight (Shaddish and Haddock 1994, Hedges *et al.* 1999).

Variation in effect size (Q_T) can be partitioned into within-experiment variation (Q_{wi}), and between-experiment variation (Q_b) (see Hedges *et al.* 1999 for further detail). Q_b is tested by the homogeneity statistic, Q, with the null hypothesis that the between-experiment variance (Q_b) is zero rejected whenever Q exceeds the 100(1 - α) percentage point on the chi-squared distribution (Hedges *et al.* 1999, Huedo-Medina *et al.* 2006). That is, if the null-hypothesis of Ra'ui effects being homogenous is rejected, then the response of Ra'ui is heterogeneous across sites i.e., Ra'ui effect sizes vary. The meta-analysis used in this study addresses whether there are consistent responses to Ra'ui across sites, and whether general inferences of Ra'ui effects are appropriate at the level of either species or functional groups.

b) Partitioning variation with ANCOVA

Two-factor ANCOVA models using a blocked design (each site's Ra'ui / Control pair constitutes a block) were used to quantify the sources of variation in densities of fish, invertebrates and functional groups (see *a* above). Square-root transformed density was the response variable, protection and site were the fixed factors (the interaction between level of protection and site was also evaluated) and substrate 'usability index' (*S*), the covariate. A post-hoc power analysis was carried out using the R statistical platform (R Development Core Team 2006). However, the blocking factor ("site') had to be removed from the ANCOVA to maintain a balanced design for power analysis (as data was gathered from only 5 transects in each Ra'ui / Control pair at Matavera, but from 10 transects in each Ra'ui / Control pair at the 5 other sites).

How data were constrained for analysis

To investigate responses of individual species to Ra'ui, I constrained my available data to species that were present at most of the sites across my sampling areas (see Appendix A, Table 1 for list including common and Cook Islands Māori names) For fish species, the criteria for inclusion was being present at more than 10 of the 12 sites, for invertebrates being present at greater than 5 of the 12 lagoon sites, and at more than 3 of the 4 reef crest sites. 21 of the recorded 136 species of fish, 14 of the 18 lagoon invertebrate species, and 11 of the 18 reef crest fauna met these criteria and were retained for analyses.

To examine variation in the responses of functional groups to Ra'ui, each of the 136 originally censused fish species were assigned to functional groups based on adult diet (Randall 1965, Froese and Pauly 2008). The assignment of species to functional groups, and the difficulties therein, have engendered much debate (Parrish 1989, Jones 1991). I therefore explored two levels of aggregation: broad-scale (based on Halpern 2003), and fine-scale (based on Floeter *et al.* 2006). The broad-scale approach used four categories: carnivores, planktivore/invertebrate feeders, omnivores, and herbivores. The fine-scale approach functional used eight categories: piscivores (feed on fish only), carnivores (feed on both fish and invertebrates), sessile invertebrate feeders (feed on sessile invertebrates), omnivores (feed on animal and algal material), mobile invertebrate feeders (feed on mobile invertebrates), planktivores, territorial herbivores, and roving herbivores.

RESULTS

Responses of individual fish species to Ra'ui

Fish species showed inconsistent responses to Ra'ui; both across species within a site, and by species across sites (Figure 3.1a). No species appeared to have consistently greater or lesser abundances inside relative to outside the Ra'ui across all sites. Responses to Ra'ui differed between sites for all of the 22 species included in the analysis (Figure 3.1a), and for 14 of the fish species sampled, Ra'ui did not share a statistically significant common effect size (Table 3.1).

Responses within families varied between species (Figure 3.1a). Of the four Acanthurids (all roving herbivores) included in the analysis, *Ctenochaetus striatus*, had significantly greater abundances in the Akapuao, and Parliament Ra'ui, and lower abundances in the Tikioki Ra'ui relative to Control sites, while abundances were similar inside and outside Ra'ui at the other three sites. Abundances of

Acanthurus triostegus were significantly greater inside Tikioki Ra'ui, and similar inside and outside Ra'ui at all other sites (Figure 3.1). Abundances of *Naso lituratus* were similar inside and outside the Ra'ui across all sites, while *Naso unicornis* had higher abundances inside Akapuao and Parliament Ra'ui, but lower abundances at Matavera Ra'ui (at all other sites confidence intervals overlapped zero) (Figure 3.1). Labrids and Siganids, had variable responses to Ra'ui, while the Chaetodontids all had similar abundances inside and outside Ra'ui, except at Tikioki Ra'ui where *Chaetodon citrinellus* had significantly lower abundances inside the Ra'ui than the corresponding Control sites (Figure 3.1). Only one of the two goatfish species, *Parupeneus multifasciatus*, had significantly higher abundances inside Ra'ui, at only one site, Parliament, and significantly lower abundances inside Ra'ui at Tikioki. The other goatfish species, *Mulloidichthys flavolineatus*, had significantly lower abundances at Aroa and Matavera Ra'ui (Figure 3.1). Both goatfish species had similar abundances inside and outside Ra'ui at all remaining sites (Figure 3.1). The parrotfish, *Chlorurus sordidus*, had similar abundances inside and outside Ra'ui, except at Aroa Ra'ui, where abundance was significantly lower inside the Ra'ui compared to the corresponding control site (Figure 3.1). *Epinephelus hexagonatus* had lower or similar densities within Ra'ui relative to Control sites, except at Aroa Ra'ui where *E. hexagonatus* was found inside the Ra'ui but was absent from the corresponding Control site (Figure 3.1).

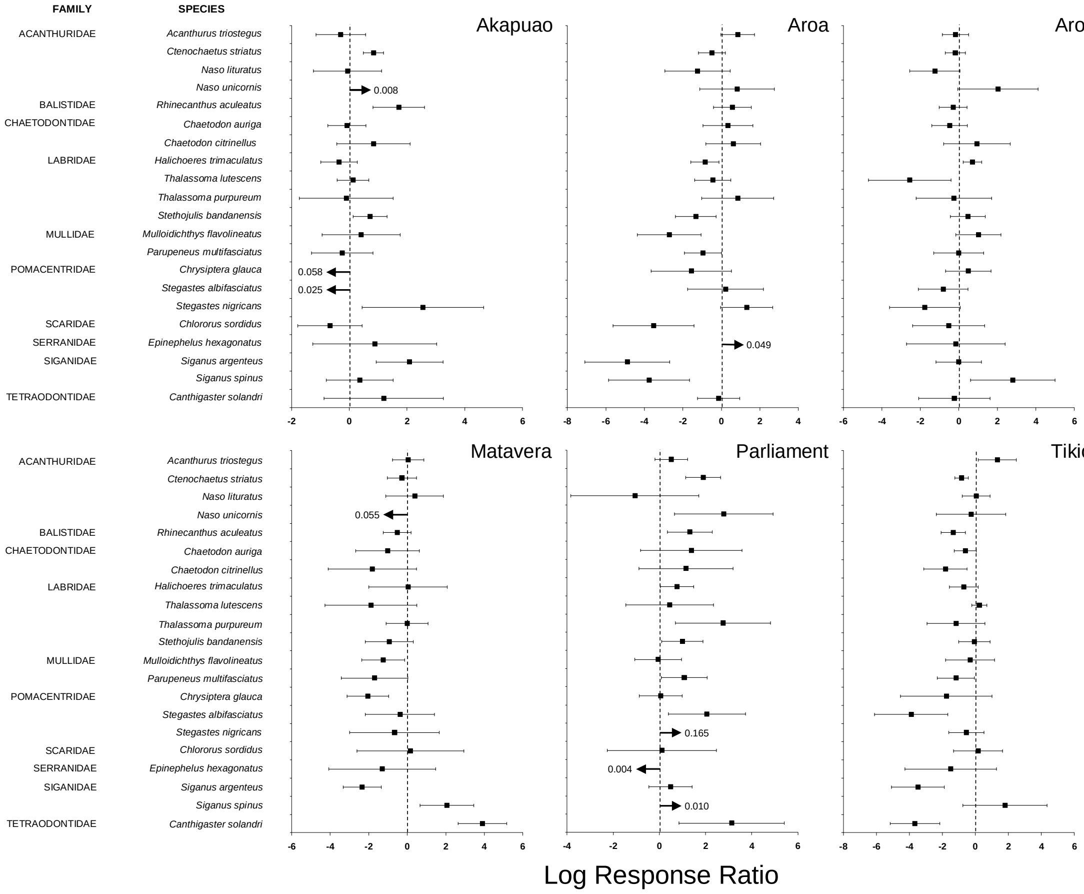


Figure 3.1. Log response ratios for 21 fish species in the lagoon at each of the six Ra'ui (error bars are +/- 95% confidence intervals). Where there is no data point for a species, it was not possible to calculate a response ratio due to absence of the species at both the Ra'ui and corresponding Control site. Where the species was present in only the Impact or Control site but not both, ← indicates the 'adjusted' density could only be determined for the Control site while →indicates the 'adjusted' density could only be determined for the Ra'ui site. As a response ratio could not be calculated in these cases, the mean 'substrate-adjusted' density is indicated beside the arrows.

Table 3.1. The effect size (weighted mean of the response ratio) with 95% confidence intervals, the ratio of within-site variation (Q_{wi}) to between-site variation (Qb), and the homogeneity statistic (Q) calculated across all Ra'ui for each lagoon fish and invertebrate species. * indicates statistical significance following a chi-square test. If Q is greater than the critical value (Critical value for 5 df and alpha = 0.05 is 11.070), the null hypothesis of no difference in variance between Ra'ui is rejected (i.e., there is significant heterogeneity in response to protection between Ra'ui).

Family	**Scientific Name**	**Effect Size (95% CI)**	**Ratio (Q_b /Q_{wi})**	**Q**	**Heterogenous?**
FISH					
ACANTHURIDAE	*Acanthurus triostegus*	0.305 (-0.994, 1.605)	0.713	9.032	
	Ctenochaetus striatus	0.143 (-0.673, 0.959)	5.993	47.343	*
	Naso lituratus	-0.334 (-3.021, 2.354)	0.08	5.611	
	Naso unicornis	1.333 (-1.579, 4.245)	1.617	8.280	
BALISTIDAE	*Rhinecanthus aculeatus*	0.206 (-0.863, 1.275)	4.996	31.272	*
CHAETODONTIDAE	*Chaetodon auriga*	-0.264 (-2.443, 1.914)	0.093	5.827	
	Chaetodon citrinellus	0.017 (-2.243, 2.276)	1.150	11.769	*
LABRIDAE	*Halichoeres trimaculatus*	-0.036 (-1.484, 1.412)	1.052	15.549	*
	Thalassoma lutescens	-0.183 (-2.582, 2.216)	0.284	9.236	
	Thalassoma purpureum	0.246 (-2.282, 2.774)	0.626	8.372	
	Stethojulis bandanensis	0.064 (-1.121, 1.248)	1.886	15.859	*
MULLIDAE	*Mulloidichthys flavolineatus*	-0.406 (-2.181, 1.369)	1.706	14.521	*
	Parupeneus multifasciatus	-0.437 (-2.045, 1.172)	1.463	13.649	*
POMACENTRIDAE	*Chrysiptera glauca*	-0.769 (-3.258, 1.721)	1.125	11.644	*
	Stegastes albifasciatus	-0.477 (-2.786, 1.832)	2.491	16.175	*
	Stegastes nigricans	0.154 (-2.252, 2.560)	1.529	11.747	*
SCARIDAE	*Chlororus sordidus*	-0.714 (-3.134, 1.705)	0.902	10.569	
SERRANIDAE	*Epinenephelus hexagonatus*	-0.688 (-3.491, 2.115)	5.102	47.423	*
SIGANIDAE	*Siganus argenteus*	-1.236 (-3.245, 0.772)	8.306	59.072	*
	Siganus spinus	0.647 (-1.924, 3.219)	3.986	23.257	*
TETRAODONTIDAE	*Canthigaster solandri*	0.663 (-1.640, 2.967)	8.071	54.663	*
INVERTEBRATES					
DIADEMATIDAE	*Diadema savignyi*	1.752 (-2.651, 6.154)	5.780	16.042	*
	Echinothrix diadema	1.594 (-1.537, 4.726)	2.339	12.217	*
ECHINOMETRIDAE	*Echinometra mathaei*	-0.368 (-1.495, 0.759)	3.932	30.184	*
	Echinometra oblonga	-1.416 (-5.054, 2.223)	0.948	4.761	
HOLOTHURIIDAE	*Actinopyga mauritiana*	1.754 (-2.287, 5.795)	4.534	5.534	
	Holothuria atra	-0.102 (-1.553, 1.349)	3.807	30.601	*
	Holothuria cinerascens	1.941 (-2.051, 5.933)	0.939	3.873	
	Holothuria leucospilota	-0.536 (-2.422, 1.350)	10.397	89.587	*
OPHIDIASTERIDAE	*Linckia laevigata*	0.492 (-4.604, 5.588)	-0.218	1.243	
STICHOPODIDAE	*Stichopus chloronotus*	0.222 (-2.015, 2.459)	1.824	15.896	*
TOXOPNEUSTIDAE	*Tripneustes gratilla*	0.677 (-3.111, 4.465)	0.086	3.335	
TRIDACNIDAE	*Tridacna spp.*	0.315 (-1.556, 2.187)	3.501	27.002	*
TROCHIDAE	*Trochus niloticus*	1.364 (-0.828, 3.557)	2.003	9.367	
VERMETIDAE	*Dendropoma maxima*	0.963 (-1.659, 3.585)	1.631	12.322	*

Responses of individual invertebrate species to Ra'ui

Lagoon invertebrates exhibited inconsistent responses to Ra'ui, both within Ra'ui (i.e., all species did not share the same response to protection within a Ra'ui), and across Ra'ui (i.e., across all Ra'ui, a single species did not have a consistent response to protection) (Figure 3.2). Ra'ui did not share a statistically significant common effect size for around 60% of the invertebrate species sampled (Table 3.1).

The Diadematid urchins, *Diadema savignyi* and *Echinothrix diadema*, both had significantly greater abundances inside Aroa Ra'ui but significantly lower abundances at Aroko Ra'ui relative to Control sites (Figure 3.2). Giant clam species (*Tridacna* spp.) had significantly greater abundances in the Akapuao, Aroa and Parliament Ra'ui than at corresponding Control sites (Figure 3.2). Abundances of *Trochus niloticus* were similar at all Ra'ui relative to Control sites, except at Aroko Ra'ui where *T. niloticus* occurred in the Ra'ui but not at the control site (Figure 3.2). The vermetid snail, *Dendropoma maxima*, was significantly more abundant inside the Aroa Ra'ui relative to the Control site with abundances at all other sites were similar in Ra'ui and Controls, except for Aroko and Parliament Ra'ui, where *D. maxima* did not occur at the corresponding Control sites (Figure 3.2).

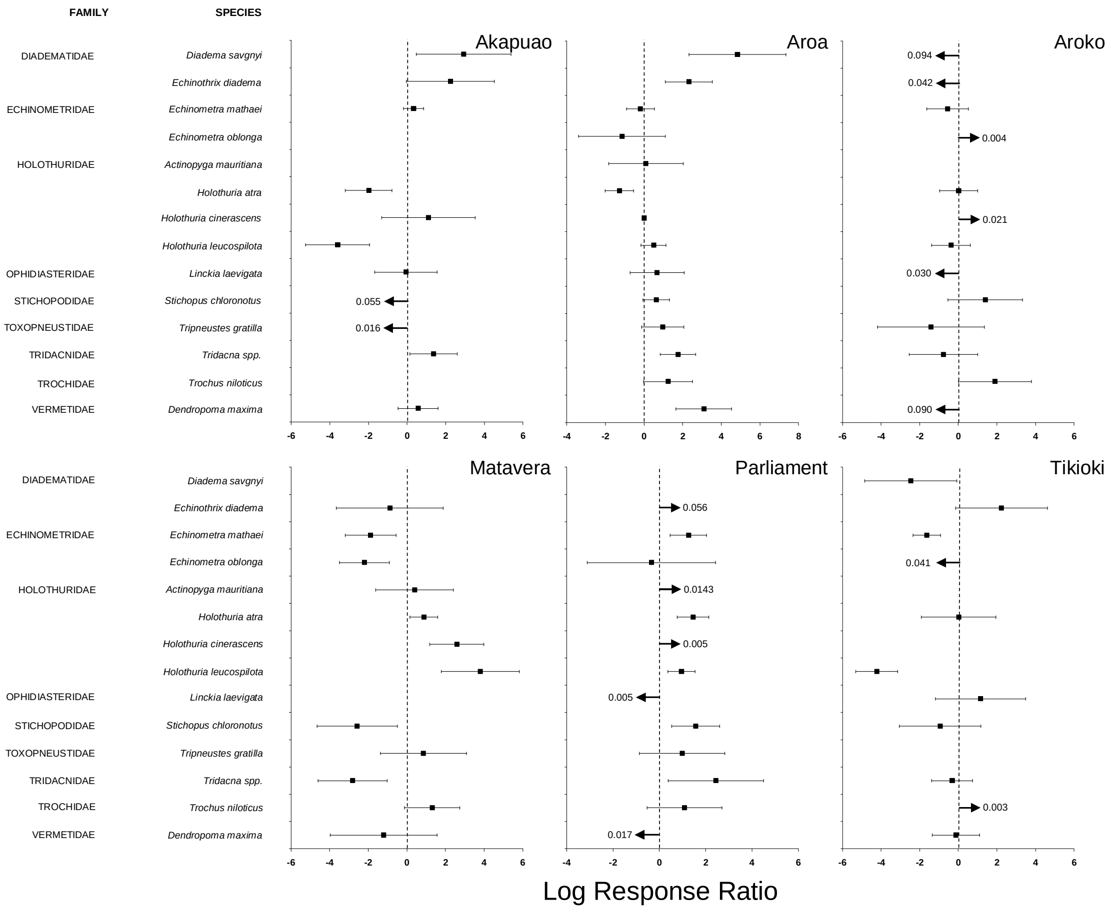


Figure 3.2. Log response ratios for 14 invertebrate species at each of the six Ra'ui (lagoon only) (error bars are +/- 95% confidence intervals). Where there is no data point for a species, it was not possible to calculate a response ratio due to absence of the species at both the Ra'ui and corresponding Control site. Where the species was present in only the Impact or Control site but not both, ← indicates the 'adjusted' density could only be determined for the Control site while → indicates the 'adjusted' density could only be determined for the Ra'ui site. As a response ratio could not be calculated in these cases, the mean 'substrate-adjusted' density is indicated beside the arrows.

Invertebrates at the two reef crest sites also demonstrated variable responses to Ra'ui (Figure 3.3). *Holothuria cinerascens* and *Trochus niloticus* had greater abundances inside relative to outside at both Ra'ui, while *Echinothrix diadema,* and *Actinopyga mauritiana* had consistently similar abundances inside and outside Ra'ui across all sites (Figure 3.3). Urchins at Matavera Ra'ui tended to have the opposite response to those in the Parliament Ra'ui, with urchins generally more abundant in the Matavera Ra'ui and less abundant in the Parliament Ra'ui relative to Control sites (Figure 3.3). *Turbo setosus* abundances were similar inside and outside the Matavera Ra'ui, with none present inside the Parliament Ra'ui, only outside. *Dendropoma maxima* only occurred inside the Matavera Ra'ui, with none occurring outside.

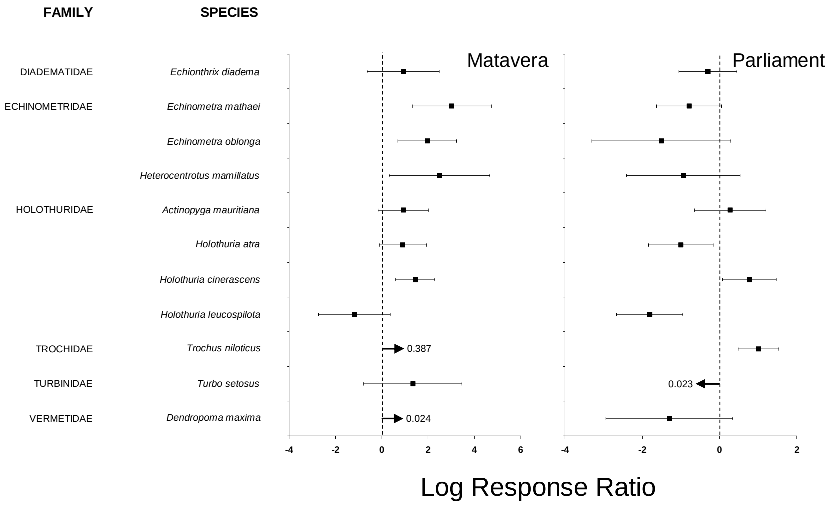


Figure 3.3. Log response ratios for 11 invertebrate species at two Ra'ui (reef crest only) (error bars are +/- 95% confidence intervals). Where there is no data point for a species, it was not possible to calculate a response ratio due to absence of the species at both the Ra'ui and corresponding Control site. Where the species was present in only the Impact or Control site but not both, ← indicates the 'adjusted' density could only be determined for the Control site while → indicates the 'adjusted' density could only be determined for the Ra'ui site. As a response ratio could not be calculated in these cases, the mean 'substrate-adjusted' density is indicated beside the arrows.

Effects of Ra'ui on lagoon species by site

More lagoon invertebrates had higher abundances inside Ra'ui relative to Control sites, than fish (Figure 3.4). On average, 15% of fish species, and 20% of the invertebrate species had significantly higher (95% confidence interval did not overlap zero) abundances inside Ra'ui than corresponding Control sites (Figure 3.4). Abundances for 43% of the fish and 38% of the invertebrates were significantly higher inside the Parliament Ra'ui relative to Control sites. At Akapuao Ra'ui, 24% of the fish had higher abundances inside than outside the Ra'ui. Of all Ra'ui, Aroa, Aroko, Tikioki and Matavera had the lowest percentage of fish species (< 10%), and Aroko, and Tikioki had the lowest percentage of invertebrate species (0%) with lower abundances inside the Ra'ui than the corresponding Control (Figure 3.4).

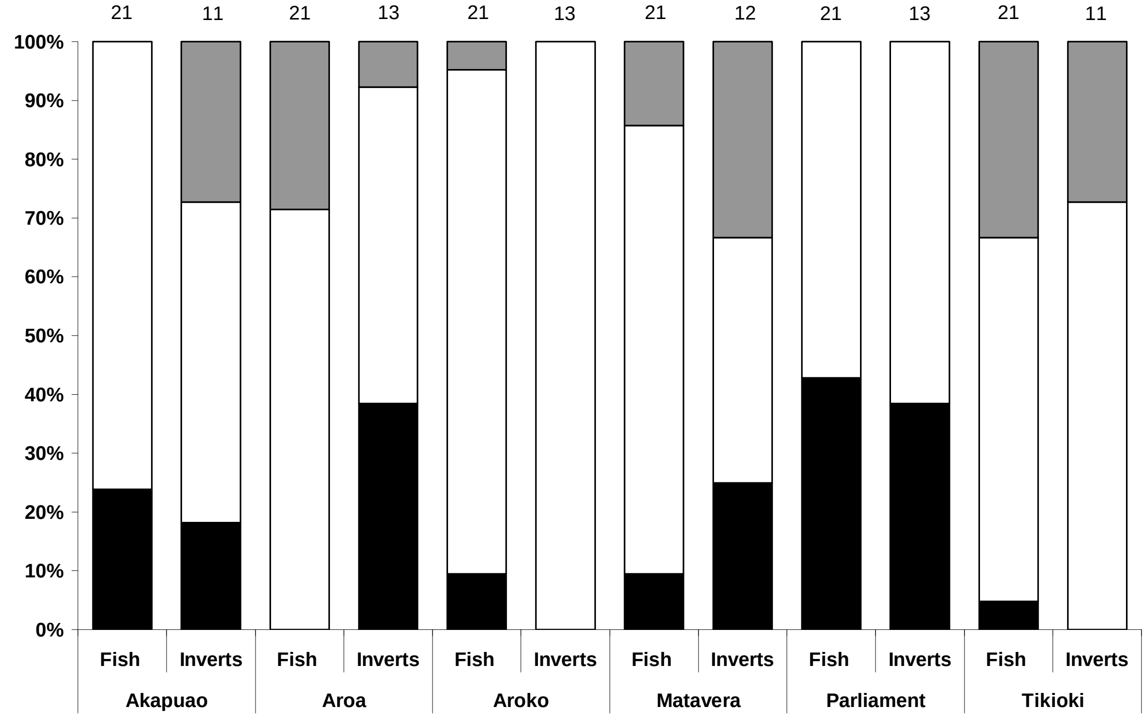


Figure 3.4. The percentage of fish and invertebrate species having significantly greater (■), lesser (▨), and statistically indistinguishable (□) abundances inside Ra'ui relative to corresponding Control sites at six sites (lagoon only). Where fish or invertebrates were present inside the Ra'ui but not outside, and vice-versa (see Figures 3.2, 3.3 & 3.4), a non-parametric Mann-Whitney U test assessed whether these Ra'ui and Control abundances were significantly different. The total number of species per site is represented by 'n' at the top of each bar.

Fine-scale and broad-scale fish functional group responses

At the fine-scale level of categorisation, no functional groups had consistently higher or lower abundances inside Ra'ui relative to Control sites, with heterogeneous effect sizes across Ra'ui (Figure 3.5). Carnivores had higher abundances inside Ra'ui than at Control sites at only one site, Parliament, while Piscivores had higher abundances inside Ra'ui than at Control sites over the greatest number of sites (3 sites) (Figure 3.5). Planktivores, territorial herbivores, and sessile invertebrate feeders generally had similar abundances inside Ra'ui and Control sites (4, 4, and 5 sites respectively), while the response of both omnivores and roving herbivores responses were split, displaying higher (omnivores at Parliament; roving herbivores at Akapuao and Aroko), similar (omnivores at Akapuao, Aroko and Aroa, roving herbivores at Aroko, Parliament and Tikioki), and lower (omnivores at Tikioki and Matavera, roving herbivores at Aroa and Matavera) abundances within Ra'ui compared to Control sites (Figure 3.5). Five out of the eight fine-scale functional groups had a statistically significant heterogeneous responses to Ra'ui (Table 3.2).

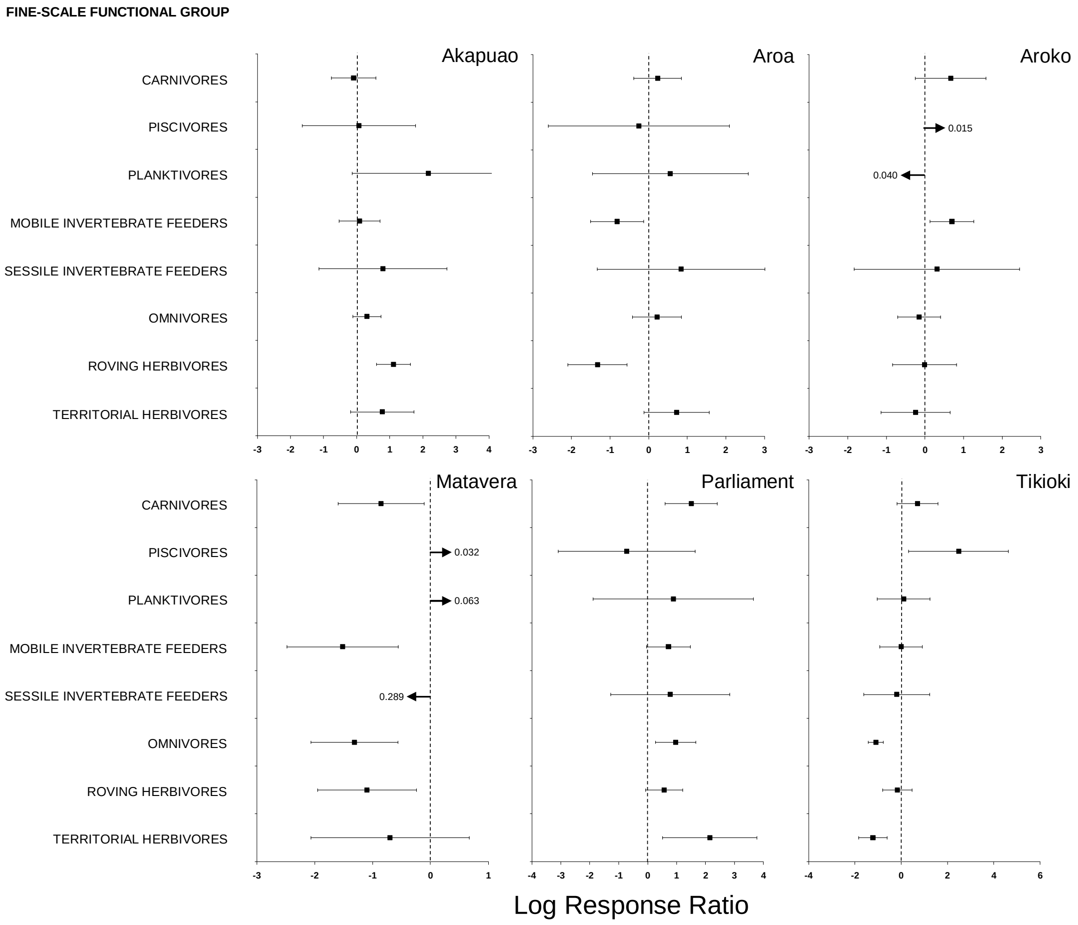


Figure 3.5. Log response ratios of eight fine-scale fish functional groups at each of the six Ra'ui (error bars are +/- 95% confidence intervals). Where there is no data point for a functional group, it was not possible to calculate a response ratio due to absence of the functional group at both the Ra'ui and corresponding Control site. Where the functional group was present in only the Impact or Control site but not both, ← indicates the 'adjusted' density could only be determined for the Control site while → indicates the 'adjusted' density could only be determined for the Ra'ui site. As a response ratio could not be calculated in these cases, the mean 'substrate-adjusted' density is indicated beside the arrows.

Table 3.2. Ratio of within-site variation (Q_{wi}) to between-site variation (Qb), and the homogeneity statistic (Q) calculated across all Ra'ui for each broad- and fine-scale fish functional group. * indicates statistical significance following a chi-square test. If Q is greater than the critical value (Critical value for 5 df and alpha = 0.05 is 11.070), then reject H_0 that there is no difference in variance (variance is homogenous) between Ra'ui i.e., there is significant heterogeneity in response to protection between Ra'ui.

Functional Group	**Effect Size (95% CI)**	**Ratio (Q_b / Q_{wi})**	***Q***	**Heterogenous?**
FINE-SCALE				
Carnivores	0.331 (-0.679, 1.341)	2.314	17.303	*
Piscivores	0.415 (-3.244, 4.074)	0.390	4.217	
Planktivores	0.637 (-3.129, 4.404)	0.130	3.540	
Mobile Invertebrate Feeders	-0.051 (-1.113, 1.011)	1.896	16.633	*
Sessile Invertebrate Feeders	-0.591 (-7.266, 6.084)	-0.540	1.594	
Omnivores	-0.173 (-0.976, 0.630)	5.178	40.329	*
Roving Herbivores	-0.108 (-1.035, 0.818)	4.172	28.732	*
Territorial Herbivores	0.134 (-1.248, 1.516)	2.360	20.845	*
BROAD-SCALE				
Carnivores	0.335 (-0.702, 1.373)	1.693	14.095	*
Planktivores / Invertebrate feeders	-0.010 (-1.028, 1.008)	1.999	17.377	*
Omnivores	-0.177 (-0.997, 0.643)	7.332	43.968	*
Herbivores	-0.093 (-0.969, 0.784)	4.467	28.748	*

Broad-scale functional group responses were similar to fine-scale functional group responses, with no consistently higher or lower abundances inside relative to outside Ra'ui (Figure 3.6). Carnivores had significantly higher abundances (confidence intervals did not span zero) inside Ra'ui at the greatest number of sites (two sites), while carnivores and planktivores had similar abundances inside and outside Ra'ui at four sites each (Figure 3.6). The responses of herbivores were split across Ra'ui between higher (Akapuao), equal (Aroko, Parliament, and Tikioki) and lower (Aroa and Matavera) abundances inside Ra'ui relative to Control sites. All broad-scale functional groups had a statistically significant heterogeneous response to Ra'ui (Table 3.2).

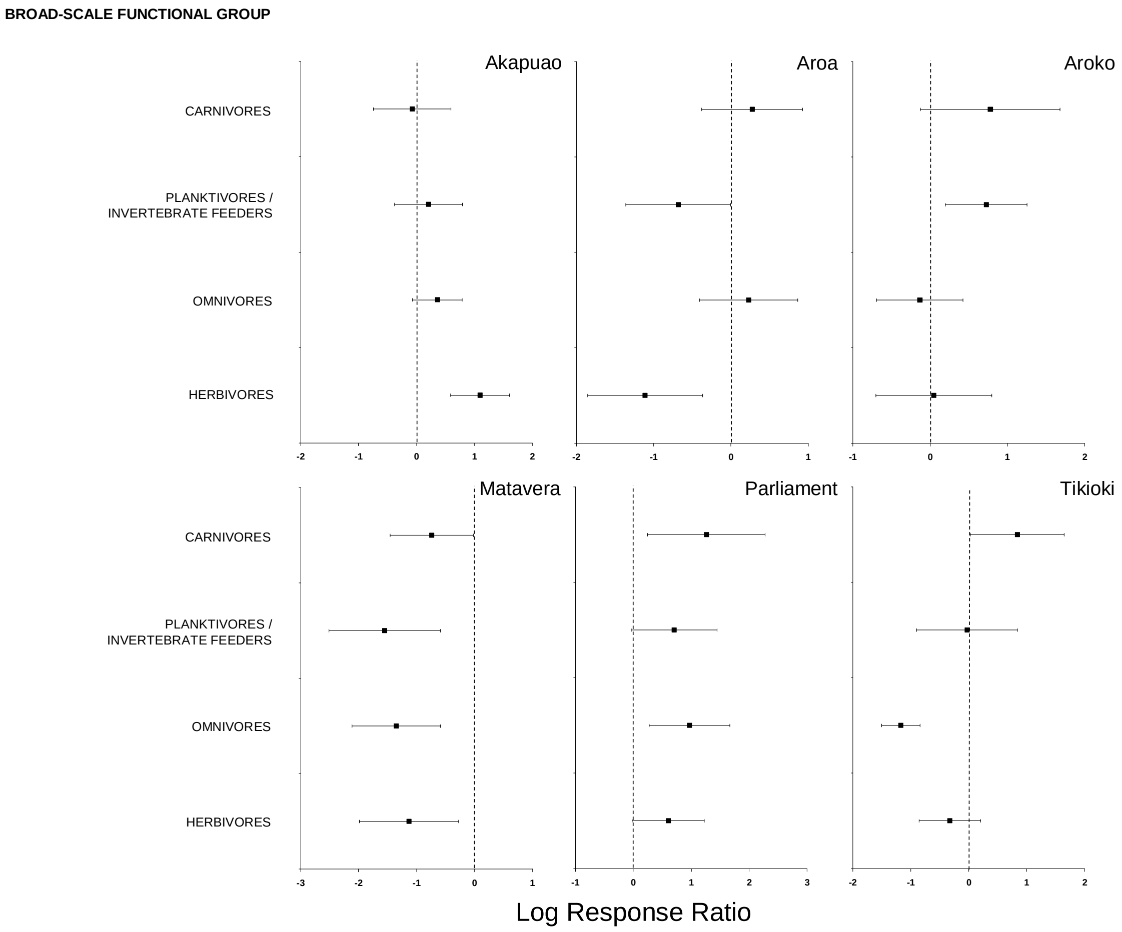


Figure 3.6. Log response ratios of four broad-scale fish functional groups at each of the six Ra'ui (error bars are +/- 95% confidence intervals). Where there is no data point for a functional group, it was not possible to calculate a response ratio due to absence of the functional group at both the Ra'ui and corresponding Control site. Where the functional group was present in only the Ra'ui or Control site but not both, ← indicates the 'adjusted' density could only be determined for the Control site while → indicates the 'adjusted' density could only be determined for the Ra'ui site. As a response ratio could not be calculated in these cases, the mean 'substrate-adjusted' density is indicated beside the arrows.

Meta-analyses of fish, invertebrates, and functional group responses to Ra'ui

Meta-analysis assessed whether there was an overall Ra'ui effect for each individual fish, invertebrate species, and functional group across all sites combined. Island-wide, neither fish, invertebrates, nor functional groups exhibited overall increased or decreased abundances inside relative to outside Ra'ui.

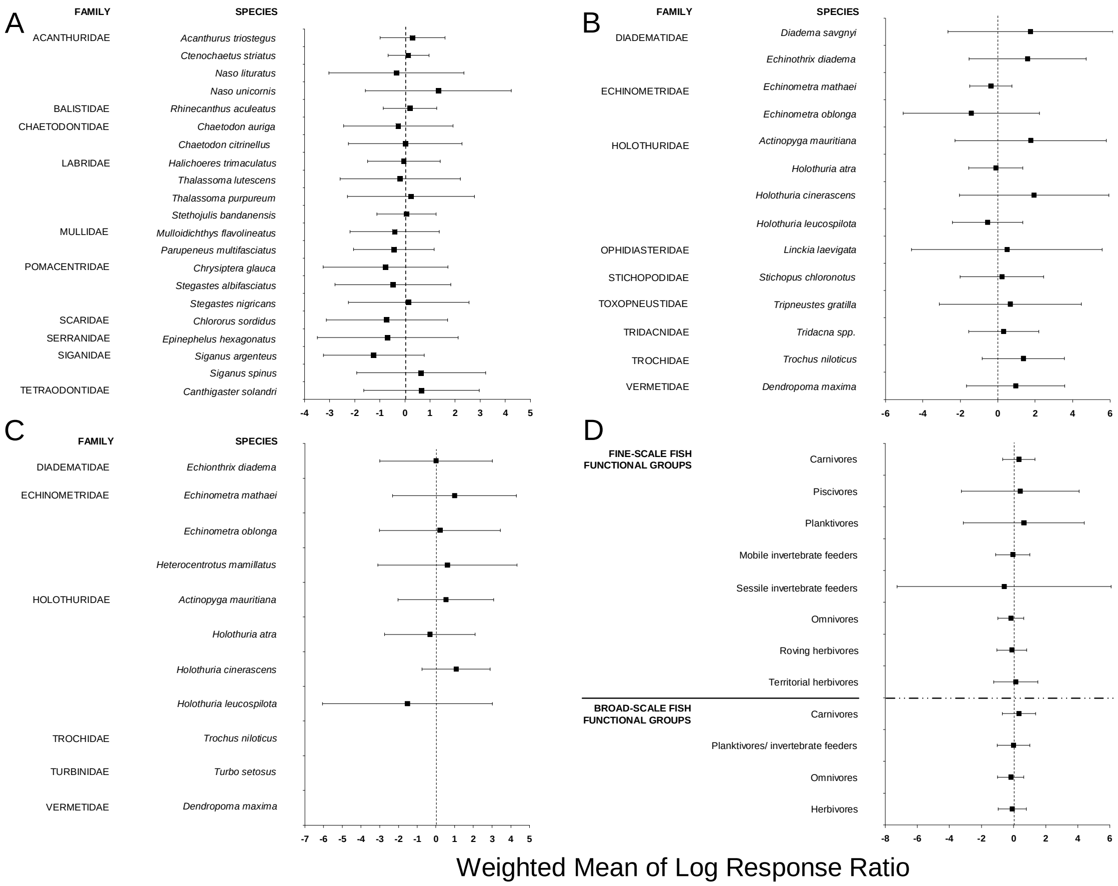


Figure 3.7. Meta-analysis of response ratios showing weighted mean of log response ratios for lagoon fish (A) and invertebrates (B), reef crest invertebrate species (C), and, fine-scale and broad-scale functional fish groups (D) across all Ra'ui ("Island-wide"). Error bars are +/- 95% confidence intervals. Note: a weighted mean could not be calculated where reef crest invertebrate species (C) only occurred at one of the two reef crest sites.

Direct test of an overall Ra'ui effect

Fish

Contrary to the meta-analyses above, blocked two factor ANCOVA models, with level of protection and site as fixed factors, and 'usable substrate' as covariate, indicated that protection determined a significant amount of variation in densities for 6 (*Rhinecanthus aculeatus*, *Parupeneus multifasciatus*, *Chrysiptera glauca*, *Stegastes nigricans*, *Chlorurus sordidus*, and *Siganus spinus*) of the 21 fish species throughout the lagoon (Table 3.3). However, for 4 (*R. aculeatus*, *C. glauca*, *C. sordidus*, and *S. spinus*) of the 6 species, there was also a significant interaction between the level of protection (i.e., Ra'ui versus Control) and site (Table 3.3). There were only 5 fish species (*Naso unicornis*, *Stethojulis bandanensis*, *Parupeneus multifasciatus*, *Stegastes nigricans*, and *Epinephelus hexagonatus*) where site did not determine a significant amount of variation in densities throughout the lagoon (Table 3.3). Again, for 12 of the 16 species where site was significant in determining variation in fish densities, there was also a significant interaction between the level of protection and site (Table 3.3). Substrate was significant in determining variation in densities for 10 of the 21 fish species in the lagoon (Table 3.3). Level of protection alone determined a significant amount of variation in densities of the goatfish, *Parupeneus multifasciatus*, in the lagoon around Rarotonga, while level of protection and substrate accounted for significant variation in densities of the dusky gregory, *Stegastes nigricans*.

Power was adequate for detecting an effect of protection for 19 of the 21 fish species (i.e., power $(1-\beta) \geq 0.8$), except for two species, the unicornfish, *Naso unicornis*, and the goatfish, *Parupeneus multifasciatus* (Table 3.3). Power for *N. unicornis* was low, indicating that although no significant effect of protection was observed, with increased sampling, there may be a detectable effect (Table 3.3). Alternately, power was also low for *P. multifasciatus*, but there was a significant effect of protection for this species.

Table 3.3. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of lagoon fish species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	**Treatment**	**df**	**MS**	**F-ratio**	**p**	**Power (1-β)**
Acanthurus triostegus	Full model	12	0.118	4.269	p<0.001	*
	Protection	1	0.086	3.101	0.081	
	Site	5	0.083	2.980	0.015	
	Substrate	1	0.359	12.925	0.001	
	Protection X Site	5	0.031	1.109	0.361	
	Error	97	0.028			
Ctenochaetus striatus	Full model	12	0.208	11.139	p<0.001	*
	Protection	1	0.037	1.985	0.162	
	Site	5	0.195	10.465	p<0.001	
	Substrate	1	0.935	50.053	p<0.001	
	Protection X Site	5	0.065	3.489	0.006	
	Error	97	0.019			
Naso lituratus	Full model	12	0.012	3.147	0.001	0.143
	Protection	1	0.000	0.014	0.905	
	Site	5	0.020	5.149	p<0.001	
	Substrate	1	0.003	0.703	0.404	
	Protection X Site	5	0.007	1.891	0.103	
	Error	97	0.004			
Naso unicornis	Full model	12	0.008	1.442	0.160	*
	Protection	1	0.011	2.063	0.154	
	Site	5	0.009	1.626	0.160	
	Substrate	1	0.005	1.020	0.315	
	Protection X Site	5	0.006	1.119	0.355	
	Error	97	0.005			
Rhinecanthus aculeatus	Full model	12	0.029	5.490	p<0.001	*
	Protection	1	0.037	6.900	0.010	
	Site	5	0.037	7.070	p<0.001	
	Substrate	1	0.004	0.671	0.415	
	Protection X Site	5	0.014	2.595	0.030	
	Error	97	0.005			
Chaetodon auriga	Full model	12	0.014	2.373	0.010	*
	Protection	1	0.003	0.518	0.473	
	Site	5	0.027	4.792	0.001	
	Substrate	1	0.003	0.577	0.449	
	Protection X Site	5	0.003	0.557	0.733	
	Error	97	0.006			
Chaetodon citrinellus	Full model	12	0.005	1.503	0.136	*
	Protection	1	0.001	0.438	0.510	
	Site	5	0.009	2.802	0.021	
	Substrate	1	0.001	0.285	0.594	
	Protection X Site	5	0.003	0.794	0.556	
	Error	97	0.003			
Halichoeres trimaculatus	Full model	12	0.098	11.425	p<0.001	*
	Protection	1	0.005	0.609	0.437	
	Site	5	0.086	10.028	p<0.001	
	Substrate	1	0.381	44.412	p<0.001	
	Protection X Site	5	0.030	3.502	0.006	
	Error	97	0.009			

Table 3.3 continued. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of lagoon fish species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	Treatment	df	MS	F-ratio	p	Power (1-β)
Thalassoma lutescens	Full model	12	0.067	14.048	p<0.001	*
	Protection	1	0.011	2.419	0.123	
	Site	5	0.131	27.596	p<0.001	
	Substrate	1	0.014	2.980	0.087	
	Protection X Site	5	0.023	4.934	p<0.001	
	Error	97	0.005			
Thalassoma purpureum	Full model	12	0.036	11.310	p<0.001	*
	Protection	1	0.012	3.655	0.059	
	Site	5	0.039	12.277	p<0.001	
	Substrate	1	0.059	18.439	p<0.001	
	Protection X Site	5	0.009	2.936	0.016	
	Error	97	0.003			
Stethojulis bandanensis	Full model	12	0.019	4.242	p<0.001	*
	Protection	1	0.000	0.009	0.924	
	Site	5	0.005	1.214	0.309	
	Substrate	1	0.106	23.556	p<0.001	
	Protection X Site	5	0.010	2.288	0.052	
	Error	97	0.005			
Mulloidichthys flavolineatus	Full model	12	0.136	3.674	p<0.001	*
	Protection	1	0.000	0.012	0.915	
	Site	5	0.149	4.044	0.002	
	Substrate	1	0.262	7.080	0.009	
	Protection X Site	5	0.099	2.686	0.026	
	Error	97	0.037			
Parupeneus multifasciatus	Full model	12	0.009	1.122	0.352	0.115
	Protection	1	0.043	5.136	0.026	
	Site	5	0.003	0.372	0.867	
	Substrate	1	0.007	0.878	0.351	
	Protection X Site	5	0.013	1.543	0.184	
	Error	97	0.008			
Chrysiptera glauca	Full model	12	0.093	10.508	p<0.001	*
	Protection	1	0.039	4.438	0.038	
	Site	5	0.058	6.497	p<0.001	
	Substrate	1	0.453	51.106	p<0.001	
	Protection X Site	5	0.028	3.199	0.010	
	Error	97	0.009			
Stegastes albifasciatus	Full model	12	0.078	7.020	p<0.001	0.919
	Protection	1	0.002	0.155	0.694	
	Site	5	0.089	8.020	p<0.001	
	Substrate	1	0.309	27.889	p<0.001	
	Protection X Site	5	0.056	5.073	p<0.001	
	Error	97	0.011			
Stegastes nigricans	Full model	12	0.037	3.855	p<0.001	*
	Protection	1	0.055	5.791	0.018	
	Site	5	0.014	1.434	0.219	
	Substrate	1	0.108	11.371	0.001	
	Protection X Site	5	0.010	1.055	0.390	
	Error	97	0.010			

Table 3.3 continued. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of lagoon fish species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	Treatment	df	MS	F-ratio	p	Power (1-β)
Chlorurus sordidus	Full model	12	0.087	6.200	p<0.001	*
	Protection	1	0.070	5.007	0.028	
	Site	5	0.142	10.096	p<0.001	
	Substrate	1	0.008	0.537	0.465	
	Protection X Site	5	0.037	2.638	0.028	
	Error	97	0.014			
Epinephelus hexagonatus	Full model	12	0.003	1.517	0.131	*
	Protection	1	0.000	0.009	0.923	
	Site	5	0.001	0.719	0.611	
	Substrate	1	0.003	1.852	0.177	
	Protection X Site	5	0.004	2.233	0.057	
	Error	97	0.002			
Siganus argenteus	Full model	12	0.658	3.193	0.001	*
	Protection	1	0.581	2.823	0.096	
	Site	5	0.602	2.922	0.017	
	Substrate	1	1.484	7.206	0.009	
	Protection X Site	5	0.956	4.643	0.001	
	Error	97	0.206			
Siganus spinus	Full model	12	0.105	5.647	p<0.001	0.883
	Protection	1	0.086	4.617	0.034	
	Site	5	0.143	7.713	p<0.001	
	Substrate	1	0.016	0.837	0.363	
	Protection X Site	5	0.064	3.460	0.006	
	Error	97	0.019			
Canthigaster solandri	Full model	12	0.011	3.138	0.001	*
	Protection	1	0.006	1.751	0.189	
	Site	5	0.009	2.681	0.026	
	Substrate	1	0.000	0.116	0.734	
	Protection X Site	5	0.014	4.126	0.002	
	Error	97	0.003			

Lagoon Invertebrates

Level of protection was significant in determining variation in densities for 5 (*Echinothrix diadema, Echinometra mathaei, Actinopyga mauritiana, Holothuria cinerascens*, and *Trochus niloticus*) of the 14 lagoon invertebrate species with a significant interaction between level of protection and site for 4 of the 5 species (excluding *E. diadema*). Site accounted for variation in 13 of the 14 invertebrate species (excluding *Linckia laevigata*), again with a significant interaction between level of protection and site for 10 of the 13 invertebrate species (Table 3.4). Substrate accounted for significant variation in densities for 9 of the 14 invertebrate species (Table 3.4).

Power to detect an effect of protection was low for two of the 14 lagoon invertebrate species (Table 3.4). The urchins, *Echinometra oblonga* and *Tripneustes gratilla,* both had low power and non-significant effects of protection (Table 3.4).

Table 3.4. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of lagoon invertebrate species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	Treatment	df	MS	F-ratio	p	Power (1-β)
Diadema savignyi	Full model	12	0.034	2.383	0.010	*
	Protection	1	0.028	1.959	0.165	
	Site	5	0.037	2.625	0.029	
	Substrate	1	0.002	0.172	0.679	
	Protection X Site	5	0.037	2.590	0.030	
	Error	97	0.014			
Echinothrix diadema	Full model	12	0.017	2.809	0.002	*
	Protection	1	0.025	4.102	0.046	
	Site	5	0.022	3.638	0.005	
	Substrate	1	0.004	0.728	0.396	
	Protection X Site	5	0.011	1.754	0.130	
	Error	97	0.006			
Echinometra mathaei	Full model	12	0.880	7.235	p<0.001	*
	Protection	1	0.536	4.404	0.038	
	Site	5	1.177	9.673	p<0.001	
	Substrate	1	2.126	17.480	p<0.001	
	Protection X Site	5	0.417	3.428	0.007	
	Error	97	0.122			

Table 3.4 continued. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of lagoon invertebrate species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	Treatment	df	MS	F-ratio	p	Power (1-β)
Echinometra oblonga	Full model	12	0.010	5.428	p<0.001	0.344
	Protection	1	0.006	3.217	0.076	
	Site	5	0.019	10.652	p<0.001	
	Substrate	1	0.003	1.917	0.169	
	Protection X Site	5	0.002	1.322	0.261	
	Error	97	0.002			
Actinopyga mauritiana	Full model	12	0.016	20.227	p<0.001	0.887
	Protection	1	0.031	38.255	p<0.001	
	Site	5	0.017	20.787	p<0.001	
	Substrate	1	0.000	0.113	0.737	
	Protection X Site	5	0.014	17.816	p<0.001	
	Error	97	0.001			
Holothuria atra	Full model	12	2.766	13.339	p<0.001	*
	Protection	1	0.523	2.524	0.115	
	Site	5	5.484	26.447	p<0.001	
	Substrate	1	1.300	6.270	0.014	
	Protection X Site	5	0.846	4.080	0.002	
	Error	97	0.207			
Holothuria cinerascens	Full model	12	0.110	17.688	p<0.001	0.901
	Protection	1	0.129	20.705	p<0.001	
	Site	5	0.129	20.666	p<0.001	
	Substrate	1	0.010	1.559	0.215	
	Protection X Site	5	0.072	11.479	p<0.001	
	Error	97	0.006			
Holothuria leucospilota	Full model	12	0.942	8.380	p<0.001	*
	Protection	1	0.099	0.879	0.351	
	Site	5	1.255	11.172	p<0.001	
	Substrate	1	1.319	11.737	0.001	
	Protection X Site	5	0.801	7.132	p<0.001	
	Error	97	0.112			
Linckia laevigata	Full model	12	0.006	2.527	0.006	*
	Protection	1	0.005	2.187	0.142	
	Site	5	0.004	1.505	0.195	
	Substrate	1	0.026	10.419	0.002	
	Protection X Site	5	0.000	0.090	0.994	
	Error	97	0.003			
Stichopus chloronotus	Full model	12	0.327	18.047	p<0.001	*
	Protection	1	0.000	0.007	0.935	
	Site	5	0.693	38.306	p<0.001	
	Substrate	1	0.164	9.037	0.003	
	Protection X Site	5	0.054	2.980	0.015	
	Error	97	0.018			

Table 3.4 continued. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of lagoon invertebrate species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	Treatment	df	MS	F-ratio	p	Power (1-β)
Tripneustes gratilla	Full model	12	0.058	8.192	p<0.001	0.770
	Protection	1	0.000	0.004	0.951	
	Site	5	0.087	12.178	p<0.001	
	Substrate	1	0.092	12.901	0.001	
	Protection X Site	5	0.017	2.401	0.042	
	Error	97	0.007			
Tridacna spp.	Full model	12	0.022	4.330	p<0.001	0.974
	Protection	1	0.010	1.860	0.176	
	Site	5	0.015	2.993	0.015	
	Substrate	1	0.025	4.916	0.029	
	Protection X Site	5	0.016	3.038	0.014	
	Error	97	0.005			
Trochus niloticus	Full model	12	0.093	9.951	p<0.001	*
	Protection	1	0.179	19.071	p<0.001	
	Site	5	0.150	16.065	p<0.001	
	Substrate	1	0.040	4.302	0.041	
	Protection X Site	5	0.043	4.557	0.001	
	Error	97	0.009			
Diadema maxima	Full model	12	0.027	4.557	p<0.001	*
	Protection	1	0.020	3.396	0.068	
	Site	5	0.028	4.607	0.001	
	Substrate	1	0.053	8.799	0.004	
	Protection X Site	5	0.017	2.762	0.022	
	Error	97	0.006			

Reef Crest Invertebrates

Level of protection was significant in determining variation in the densities of 3 (*Holothuria cinerascens*, *Holothuria leucospilota*, and *Trochus niloticus*) of the 11 reef crest invertebrates (Table 3.5). Site was significant in determining variation in the densities of 5 of the 11 reef crest invertebrates, including a significant interaction between level of protection and site for *Echinometra oblonga* (Table 3.5). Substrate contributed significantly to densities of only *H. leucospilota* on the reef crest. Power to detect an effect of protection was adequate for all reef-crest invertebrates (Table 3.5).

Table 3.5. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of reef-crest invertebrate species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	Treatment	df	MS	F	p	Power (1-β)
Echinothrix diadema	Full model	4	0.483	4.417	0.015	*
	Protection	1	0.023	0.206	0.656	
	Site	1	1.556	14.234	0.002	
	Substrate	1	0.037	0.340	0.568	
	Protection X Site	1	0.001	0.007	0.934	
	Error	15	0.109			
Echinometra mathaei	Full model	4	1.194	5.520	0.006	*
	Protection	1	0.297	1.371	0.260	
	Site	1	0.696	3.216	0.093	
	Substrate	1	0.393	1.818	0.198	
	Protection X Site	1	2.686	12.415	0.003	
	Error	15	0.216			
Echinometra oblonga	Full model	4	0.861	4.464	0.014	*
	Protection	1	0.452	2.344	0.147	
	Site	1	1.388	7.198	0.017	
	Substrate	1	0.339	1.759	0.205	
	Protection X Site	1	1.762	9.132	0.009	
	Error	15	0.193			
Heterocentrotus mammillatus	Full model	4	0.007	1.074	0.404	*
	Protection	1	0.005	0.830	0.377	
	Site	1	0.002	0.338	0.569	
	Substrate	1	0.004	0.649	0.433	
	Protection X Site	1	0.019	3.058	0.101	
	Error	15	0.006			
Actinopyga mauritiana	Full model	4	0.041	2.392	0.097	0.940
	Protection	1	0.034	1.972	0.181	
	Site	1	0.097	5.654	0.031	
	Substrate	1	0.007	0.408	0.532	
	Protection X Site	1	0.000	0.001	0.972	
	Error	15	0.017			
Holothuria atra	Full model	4	0.046	1.382	0.287	*
	Protection	1	0.016	0.481	0.499	
	Site	1	0.032	0.961	0.342	
	Substrate	1	0.047	1.437	0.249	
	Protection X Site	1	0.079	2.395	0.143	
	Error	15	0.033			
Holothuria cinerascens	Full model	4	0.841	4.241	0.017	*
	Protection	1	2.767	13.961	0.002	
	Site	1	0.033	0.168	0.687	
	Substrate	1	0.141	0.712	0.412	
	Protection X Site	1	0.140	0.708	0.413	
	Error	15	0.198			

Table 3.5. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of reef-crest invertebrate species across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Scientific Name	**Treatment**	**df**	**MS**	**F**	**p**	**Power (1-β)**
Holothuria leucospilota	Full model	4	0.082	3.738	0.027	0.955
	Protection	1	0.139	6.350	0.024	
	Site	1	0.222	10.112	0.006	
	Substrate	1	0.157	7.176	0.017	
	Protection X Site	1	0.000	0.018	0.894	
	Error	15	0.022			
Trochus niloticus	Full model	4	0.276	6.601	0.003	*
	Protection	1	0.451	10.772	0.005	
	Site	1	0.565	13.489	0.002	
	Substrate	1	0.004	0.090	0.768	
	Protection X Site	1	0.002	0.045	0.834	
	Error	15	0.042			
Turbo setosus	Full model	4	0.038	2.766	0.066	*
	Protection	1	0.017	1.272	0.277	
	Site	1	0.031	2.285	0.151	
	Substrate	1	0.001	0.052	0.822	
	Protection X Site	1	0.049	3.561	0.079	
	Error	15	0.014			
Dendropoma maxima	Full model	4	0.004	0.842	0.520	0.991
	Protection	1	0.002	0.498	0.491	
	Site	1	0.000	0.000	0.986	
	Substrate	1	0.000	0.000	0.995	
	Protection X Site	1	0.011	2.683	0.122	
	Error	15	0.004			

Fine-scale Fish Functional Groups

Level of protection did not contribute to variation in any of the fine-scale fish functional group densities (Table 3.6). However, both site and substrate significantly contributed to variation in densities for carnivores, omnivores, roving herbivores, and territorial herbivores while only site contributed to variation in densities of planktivores, and substrate contributed to variation in densities of mobile invertebrate feeders (Table 3.6).

The level of power for three of the eight fine-scale functional groups was low (Table 3.6). However, although power was low for the carnivore functional group, there was practically a statistically significant effect of protection (p= 0.051) (Table 3.6).

Table 3.6. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of fine-scale functional groups across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Functional Group	Treatment	df	MS	F	p	Power (1-β)
Carnivores	Full model	12	0.078	8.363	p<0.001	0.057
	Protection	1	0.036	3.921	0.051	
	Site	5	0.072	7.732	p<0.001	
	Substrate	1	0.149	16.043	p<0.001	
	Protection X Site	5	0.017	1.783	0.123	
	Error	97	0.009			
Piscivores	Full model	12	0.003	0.537	0.886	0.991
	Protection	1	0.015	2.628	0.108	
	Site	5	0.002	0.318	0.901	
	Substrate	1	0.006	1.026	0.314	
	Protection X Site	5	0.003	0.441	0.819	
	Error	97	0.006			
Planktivores	Full model	12	0.009	2.215	0.016	*
	Protection	1	0.013	3.211	0.076	
	Site	5	0.012	2.831	0.020	
	Substrate	1	0.001	0.204	0.653	
	Protection X Site	5	0.004	0.926	0.468	
	Error	97	0.004			
Mobile Invertebrate Feeders	Full model	12	0.099	2.485	0.007	0.115
	Protection	1	0.000	0.001	0.971	
	Site	5	0.076	1.907	0.100	
	Substrate	1	0.170	4.282	0.041	
	Protection X Site	5	0.135	3.417	0.007	
	Error	97	0.040			
Sessile Invertebrate Feeders	Full model	12	0.008	2.138	0.021	0.998
	Protection	1	0.001	0.381	0.539	
	Site	5	0.005	1.376	0.240	
	Substrate	1	0.011	3.014	0.086	
	Protection X Site	5	0.010	2.822	0.020	
	Error	97	0.004			
Omnivores	Full model	12	0.051	5.736	p<0.001	0.441
	Protection	1	0.000	0.026	0.871	
	Site	5	0.027	3.029	0.014	
	Substrate	1	0.198	22.330	p<0.001	
	Protection X Site	5	0.026	2.911	0.017	
	Error	97	0.009			
Roving Herbivores	Full model	12	0.521	3.233	0.001	*
	Protection	1	0.003	0.019	0.890	
	Site	5	0.542	3.362	0.008	
	Substrate	1	2.077	12.885	0.001	
	Protection X Site	5	0.360	2.236	0.057	
	Error	97	0.161			
Territorial Herbivores	Full model	12	0.132	8.913	p<0.001	*
	Protection	1	0.001	0.057	0.811	
	Site	5	0.036	2.469	0.038	
	Substrate	1	0.963	65.221	p<0.001	
	Protection X Site	5	0.065	4.370	0.001	
	Error	97	0.015			

Broad-scale Fish Functional Groups

As with the fine-scale fish functional groups, level of protection did not contribute to variation in any of the broad-scale fish functional group densities (Table 3.7). Site was significant in determining variation in densities for carnivores, herbivores, and omnivores, while substrate significantly contributed to variation in densities of all four broad-scale functional groups (Table 3.7). For herbivores, omnivores, and planktivores / invertebrate feeders, there was a significant interaction between level of protection and site (Table 3.7). Omnivores were the only broad-scale functional group where power was low (Table 3.7).

Table 3.7. Two-factor analysis of covariance (factors = protection, and site) evaluating densities of broad-scale functional groups across all Ra'ui and Control sites, with index of 'usable substrate' (Substrate) as covariate. A post-hoc power analysis to detect an effect of protection is included where * denotes power value is ≥ 0.995

Functional Group	Treatment	df	MS	F	p	Power (1-β)
Carnivores	Full model	8	0.062	6.537	p<0.001	*
	Protection	1	0.006	0.603	0.441	
	Site	3	0.087	9.116	p<0.001	
	Substrate	1	0.051	5.365	0.024	
	Protection X Site	3	0.011	1.172	0.328	
	Error	61	0.010			
Herbivores	Full model	12	0.568	3.728	p<0.001	*
	Protection	1	0.000	0.000	0.992	
	Site	5	0.498	3.269	0.009	
	Substrate	1	2.852	18.713	p<0.001	
	Protection X Site	5	0.372	2.442	0.040	
	Error	97	0.152			
Omnivores	Full model	12	0.051	5.845	p<0.001	0.468
	Protection	1	0.000	0.034	0.854	
	Site	5	0.027	3.117	0.012	
	Substrate	1	0.204	23.271	p<0.001	
	Protection X Site	5	0.027	3.065	0.013	
	Error	97	0.009			
Planktivores / Invertebrate feeders	Full model	12	0.109	2.771	0.003	0.999
	Protection	1	0.001	0.036	0.850	
	Site	5	0.090	2.292	0.051	
	Substrate	1	0.275	6.997	0.010	
	Protection X Site	5	0.134	3.415	0.007	
	Error	97	0.039			

DISCUSSION

A priori hypotheses

Harvested fish species had significantly greater abundances inside Ra'ui relative to corresponding Control sites at only one or two of the six sites. This is contrary to the results of a recent meta-analysis examining the effects of MPAs (Mosquera *et al.* 2000). Mosquera *et al.* (2000) found that fished (=target) species were significantly more abundant inside MPAs relative to outside, while the abundance of non-target species remained similar between reserve and non-reserve areas. The variable responses of harvested invertebrate species to Ra'ui in my study also contrasts with work by Ashworth *et al.* (2004) who found densities of invertebrates targeted by fishing were greater in MPAs than reference sites. However, in this study, one Ra'ui, Aroa, appeared more effective for harvested invertebrate species than all other Ra'ui. Aroa had the highest number of harvested invertebrate species (including *Diadema savignyi*, *Echinothrix diadema*, *Tripneustes gratilla*, *Tridacna* species, and *Dendropoma maxima*) where densities were significantly higher inside the Ra'ui relative to corresponding Control sites.

Interestingly, my analyses suggest that lagoon invertebrates were more likely to exhibit stronger positive responses to Ra'ui effects relative to fish species. This is consistent with my *a priori* hypothesis and suggestions by others that marine reserves may be more effective for relatively sessile or site-attached species (e.g., many invertebrates; Parnell *et al.* 2005). However, the life-history traits (i.e., being sessile or site-attached) which could make MPAs more effective refuges for invertebrates, may also make invertebrates more vulnerable to exploitation (Ashworth *et al.* 2004, Drumm 2004). This has important implications; if compliance in MPAs is patchy, harvested invertebrates are potentially more sensitive to poaching relative to many fishes. For invertebrates on the reef crest, only the harvested marine gastropod (*Trochus niloticus*) had greater abundances at both reef crest Ra'ui relative to Control sites. I had expected that some of the harvested echinoderms such as *Echinothrix diadema* and *Heterocentrotus mammillatus* would also have greater abundances inside Ra'ui than at Control sites, but their abundances were similar inside and outside Ra'ui. Again, my finding is in contrast with one of the few studies that has looked at the effects of MPAs on harvested invertebrates where harvested invertebrates were more abundant inside the MPA than in fished zones (Ashworth *et al.* 2004).

Results from broad scale trophic classifications were similar to those for fine-scale trophic classifications: Carnivores (= predators) had significantly higher densities inside the Ra'ui relative to control sites at two Ra'ui (Parliament and Tikioki), and this pattern was nearly significant for Aroko, somewhat consistent with my *a priori* expectations, although carnivore densities were not consistently higher across all Ra'ui. The significantly greater abundances of carnivores inside Parliament and Tikioki Ra'ui are consistent with other studies where carnivores appear to have increased disproportionately in protected or lightly fished areas (Friedlander and DeMartini 2002, Graham *et al.* 2003, Sosa-Lopez *et al.* 2005). Fishing tends to remove big, long-lived species at the top of food webs (i.e., carnivores) (Pitcher 2001, Halpern and Warner 2002, Myers and Worm 2003, Rochet and Trenkel 2003). Subsequently, protection is expected to result in increased predator abundances. In my study, a number of species classified as carnivores are fished species around Rarotonga (groupers / cod, trevally (Moore 2006)) (see Appendix A, Table 2 for details of functional groupings for species). Densities of carnivores/predators were similar inside and outside Ra'ui at all other sites, contrary to my *a priori* hypothesis. In a meta-analysis of the effects of MPAs (Mosquera *et al.* 2000), fished (= target) species were significantly more abundant inside MPAs relative to outside, while the abundances of non-target species remained similar between reserve and non-reserve areas. However, a number of fished species in my study were not carnivorous (for example, goatfish, parrotfish, mullet, and drummers) but rather herbivores or planktivores / invertebrate feeders. As suggested by the response ratios in this study, planktivores /

invertebrate feeders had greater abundances at only Aroko Ra'ui, while herbivores had greater abundances at Akapuao and Parliament Ra'ui relative to control sites.

My data also provides some evidence consistent with an inverse relationship between predator and prey abundances occurring between functional groups within Ra'ui at Tikioki, Aroa, and Aroko Ra'ui, although these patterns were not biologically significant (i.e., confidence intervals for response ratios overlapped zero). Additionally, my observation of an inverse relationship between predator and prey abundances assumes that members of the other three functional groups (herbivores, omnivores, and planktivore / invertebrate feeders) comprise the prey of carnivores. Several published studies provide some evidence for subsequent decreases in prey abundance following implementation of a reserve (e.g., Williamson *et al.* 2004). For example, negative correlations between predatory species and their prey have been reported by Graham *et al.* (2003) and Sosa-Lopez *et al.* (2005), who demonstrated that the biomass of fished carnivorous species increased with protection while prey species inside MPAs decreased. Watson *et al.* (2007) found that the structure of fish assemblages between fished and protected areas differed greatly, and suggested that the removal of piscivores in fished areas results in increased abundances of prey species. Langlois *et al.* (2006) reached a similar conclusion for invertebrates, where predation by rock lobsters reduced survival of adult bivalves, suggesting the potential for trophic interactions. However, Graham *et al.* (2003) noted factors including recruitment variability, variation in habitat, and differences due to other predator effects that influence prey abundances that were not measured in their study, may confound the statistically significant negative correlations between predator and prey biomass.

There was no evidence for any inverse predator – prey relationship at the other three Ra'ui (Akapuao, Matavera, and Parliament). The lack of an inverse predator – prey relationship is consistent with inconclusive attempts to detect trophic effects such as predator–prey interactions and trophic cascades in MPAs /

fishing in coral reef ecosystems where significant decreases in piscivorous fish have not been associated with a corresponding increase in prey abundance (Jennings and Polunin 1997, Russ and Alcala 1998a, Halpern 2003).

Trophic cascades were first described by Hairston *et al.* (1960) as occurring when predators decrease the abundance of herbivores, with a subsequent increase in plant material (i.e., a food chain with three trophic levels). Further, according to Pinnegar *et al.* (2000), a trophic cascade does not necessarily have to involve plants or algae at the bottom of the food web, but may involve other trophic levels, so long as there is a tri-trophic level interaction. Although others have demonstrated trophic cascades occur in MPAs (Shears and Babcock 2003, Guidetti and Sala 2007), in my study there is no evidence of any trophic cascade occurring within either the Parliament or Tikioki Ra'ui, as my data fail to document clear decreases in abundances of other functional groups that would be consistent with a trophic cascade.

Tikioki Ra'ui had a particularly high abundance of carnivores, and this is noteworthy because the reserve is among the smallest on the island. The high densities of carnivores are somewhat surprising because carnivorous reef fishes are generally more mobile than other functional groups, and losses due to harvested spill-over might be expected to deplete populations in the Tikioki Ra'ui relative to others on the island due to the relatively small size of the Tikioki Ra'ui. In its favour, compliance at Tikioki is possibly high (it is well-known as a prime snorkelling spot on Rarotonga, with nearby residents and businesses profiting from visiting snorkelers, providing incentives for vigilance / enforcement). It is possible that higher compliance may offset the small size of Tikioki Ra'ui, and this speculation is consistent with Halpern's (2003) synthesis of MPA effects, which determined the proportional MPA effect to be independent of reserve size. As an alternative hypothesis, fish feeding that regularly occurs at Tikioki reserve (personal observations) may shape some of the patterns recorded for this Ra'ui. Previous work by Milazzo *et al.* (2005) demonstrated that fish feeding led to significant spatio-temporal changes in fish assemblages in an MPA, and suggested that an increase in predators as a result of fish feeding could result in decreased abundances of prey species. It is possible that fish feeding at Tikioki Ra'ui, coupled with the age of the Ra'ui (five years of closure to fishing at the time of my censuses) and possibly good compliance, may have played a combined role in the responses observed in my study. Good compliance may also contribute to the greater abundances of carnivores observed within Parliament Ra'ui relative to Control sites, as the Cook Islands' Parliament buildings and a number of residences are directly adjacent to Parliament Ra'ui. However, further information regarding overall fishing pressure and rates of compliance would be required for more definitive inferences.

There was no evidence for a general Ra'ui effect for any species or functional group across all sites when the data was subject to meta-analysis, contrary to my *a priori* hypothesis. However, blocked two-factor ANCOVA models indicated that island-wide, level of protection significantly contributed to variation in fish and invertebrate densities, with level of protection alone determining a significant amount of variation in densities of the goatfish, *Parupeneus multifasciatus*, the urchin, *Echinothrix diadema* (lagoon only), and the sea cucumbers, *Holothuria cinerascens*, and *Holothuria leucospilota* (reef crest only), and the gastropod, *Trochus niloticus* (reef crest only).

I suggest that the lack of concordance between the island-wide meta-analysis of Ra'ui effects (no significant effect of protection for any species or functional groups) and the blocked two-factor ANCOVA models (level of protection determined the densities for some fish and invertebrate densities (see Tables 3.3, 3.4, and 3.5), for the majority of species, is not due to lack of statistical power in my sampling design. Power can be defined as the probability of detecting a given effect in samples if the effect actually occurs in the population (Quinn and Keough 2002). Power analysis (see Tables 3.3, 3.4, 3.5, 3.6 and 3.7) indicated there was adequate power to detect an effect of protection at an island-wide scale for the majority of the fish, invertebrates, and functional groups. It is more likely that the lack of concordance between testing for an 'island-wide' effect of protection between meta-analysis and ANCOVA is an artefact relating to the combination of response ratios for each site using meta-analysis.

Meta-analyses are only 'as good' as the quality of data synthesised. A limitation of Control-Impact sampling designs is that they confound natural spatial variation (e.g., substrate heterogeneity) with the effect they are attempting to measure. This can be problematic when the results from Control-Impact assessments are incorporated into meta-analyses, which are then used to indicate the possible direction and magnitude of response to protection (reviewed by Osenberg *et al.* 2006). Although I undertook extensive efforts to statistically 'control' for potentially confounding effects of substrate heterogeneity, it is still possible that my underlying data is subject to other sources of spatial variation. Thus, the meta-analytical conclusion of 'no overall effect of Ra'ui' may, in part, be an artefact of spatial heterogeneity that was not effectively incorporated into my approach. For example, particular to each of the 6 sites, trophic interactions between species, temporal variability in sampling, and the confounding effects of spillover and larval export, along with other unmeasured factors, may have contributed to the conclusion of 'no effect' in the 'island-wide' meta-analyses. However, I suggest that the key reason there was no significant effect of Ra'ui in the meta-analyses relates to the lack of a consistent response to Ra'ui at the level of site which may be, in part, due to the aforementioned factors. For example, no lagoon fish, invertebrates, or fish functional groups exhibited consistent responses to Ra'ui across all 6 sites. When the site data were combined in a meta-analysis, those sites where species showed a positive response to Ra'ui cancelled out those sites where species showed a negative response to Ra'ui i.e., the lack of consistent responses to Ra'ui across sites led to a "cancellation effect" upon synthesis via meta-analysis.

Variation in responses to Ra'ui

My results illustrating highly variable putative responses to protection for fish and invertebrate species, and functional groups, both within Ra'ui, and across Ra'ui, were not completely unexpected. As Côté *et al.* (2001) concluded, marine reserve responses can differ significantly in their degree and direction. Willis and Anderson (2003) similarly noted that individual species or groups of species can respond positively, negatively, or have no response to protection, with a negative response not necessarily indicating a poorly functioning reserve. In addition, my *a priori* expectations were not met across all sites with responses to Ra'ui seemingly 'idiosyncratic' (*sensu* Lawton 1994) with several possible reasons for the variable responses for species and functional groups across sites.

Environmental gradients around the island of Rarotonga may play some role in determining the response of fish and invertebrates to Ra'ui. For example, Tikioki Ra'ui is at the south-east windward side of the island where the lagoon is deeper and wider, and lies between two passages open to the ocean located at Avana, and Avaavaroa. Aroa, Akapuao, and Aroko Ra'ui are also located on the windward side of the island, near large reef passages. Yet, across these windward sites, species and functional group responses to Ra'ui were not consistent. It is possible that processes governing larval and nutrient supply that may influence species abundance and composition at sites, are occurring at a higher spatial resolution than side of the island. Some current measurements have been made around Rarotonga (Holden 1992a, 1992b) but there is little information available to attribute marine circulatory patterns to observed Ra'ui effects.

Both age and size of Ra'ui may also contribute to the variability in Ra'ui effects. Commonly, the assumption is that larger MPAs are more effective, however, Halpern (2003) found the proportional effect of MPAs was independent of size. Similarly, Halpern and Warner (2002) suggested that the age of an MPA may be relatively unimportant (because responses are rapid; but see Osenberg *et* *al.* 2006 for an alternate interpretation; and work by others is contradictory, e.g., Dufour *et al.* 1995). However, the Ra'ui were all of similar age at the time of my surveys; the time since the Ra'ui were implemented or last opened to fishing was between 4.5 to 5 years. With respect to the characteristics of Ra'ui on Rarotonga, I will explore these issues in greater detail in Chapter 5.

The level of fishing outside Ra'ui, as well as the degree of compliance inside Ra'ui may also influence responses to Ra'ui. According to a fish consumption survey of households on Rarotonga (Moore 2006), 33% of the 90 households surveyed carry out some form of fishing in the lagoon; consumption of both lagoon fish and invertebrates still occurs in Rarotonga. However, it is not known if the fish and invertebrates referred to by survey participants are sourced from the lagoon on Rarotonga or from the outer islands, as there was no information on the exact location where fish and / or invertebrates were collected (Moore 2006). A more recent survey of finfish, invertebrates, and socioeconomics was carried out on Rarotonga in October 2007 (SPC 2007), indicating that only 44% of all households engage in some form of fishing. Relative to other islands in the Cook Islands, the level of fishing on Rarotonga is low, due to people leading an increasingly urban lifestyle compared with other islands in the Cook Islands, and the potential for lagoon fish to be ciguatoxic (SPC 2007). However, around 20% of the 500 households surveyed still go fishing, primarily for invertebrates such as sea cucumbers (rori, *Holothuria* spp.), giant clams (*Tridacna* spp.), urchins (vana, *Echinothrix diadema*; avake, *Tripneustes gratilla*), *Trochus niloticus*, and worm-snails (ungakoa, *Dendropoma maxima*) (SPC 2007). While carrying out the surveys for this study, I sporadically observed fishing occurring at various locations throughout the lagoon for some invertebrate and fish species including urchins (*Diadema savignyi* and *E. diadema*), sea cucumbers (rori toto, *Holothuria atra*), octopus (eke, *Octopus maorium*), and goatfish (vete, *Mulloidichthys flavolineatus*). The level of fishing outside Ra'ui may vary around the island, as may the degree of compliance within Ra'ui. Both have implications for detecting MPA effects; if little fishing occurs at Control sites relative to corresponding Ra'ui sites, then there may not be any observed effects of Ra'ui.

Finally, physical disturbance and site modification may also result in variation in responses to Ra'ui. Prior to the surveys conducted in autumn / winter 2005, a series of 5 cyclones of varying magnitude passed through Rarotonga, causing damage to coastal properties, and depositing debris (coral rubble) predominantly along the northern and eastern coasts. Previous work has shown that although cyclones result in little change to adult fish assemblages, they can lead to high juvenile mortality and redistribution of sub-adult fish (Lassig 1983), and consequently play an important role in structuring fish communities. Other work has shown that fish move from shallow to deeper waters during storms, with no overall decrease in the population or species despite habitat destruction and an eventual return to pre-cyclone community structure (Walsh 1983). It is likely that the cyclones of 2005 played a role in observed responses to Ra'ui, but to what degree is unknown as there is limited information on fish or invertebrate communities across all Ra'ui sites prior to the 2005 cyclones.

CONCLUSIONS

To summarise, a number of studies have looked at the effect of MPAs on fish community structure (Wantiez *et al.* 1997, Russ and Alcala 1998a, 1998b, Samoilys 1988, Edgar and Barrett 1999) but few have focused on multiple MPAs (Wantiez *et al.* 1997, Samoilys 1988), and even fewer have looked at the effects of a network of traditional MPAs (such as Ra'ui) in the South Pacific (this study). Furthermore, no studies have attempted a meta-analysis of the effects of MPAs across a number of sites as part of a single study (although one study was carried out using meta-analysis to examine the effects of a single MPA over a six year period (Ojeda-Martinez *et al.* 2007).

This study reinforces some of the difficulties associated with establishing causal linkages between MPAs and observed differences in species abundances between fished and protected areas. My results illustrate how apparent responses to protection (i.e., MPA effects, as estimated by Control-Impact studies) can vary even when careful attempts are made to control for habitat heterogeneity (one source of variation that potentially confounds estimates of MPA effects, see Chapter 2 for more discussion). My estimated responses of Families, of species within and among Families, and of functional groups classified according to two different published schemes, all varied within and among Ra'ui. This information is important as it implies that the effects of MPAs (assuming these are even measured by my approach) cannot always be generalised as there are a wide range of processes occurring, besides protection status and habitat heterogeneity, which can influence community structure, and fish and invertebrate abundances.

The results of this study may identify which species might best be used as 'indicator' species when assessing the effects of MPAs. If it is not possible to carry out a comprehensive survey of fish and invertebrate species to assess MPA effects, the use of 'indicator' species or 'representative' species such as goatfish (Mullidae) (Uiblein 2007) and harvested sessile invertebrate species, may be good indicators. However, the use of indicator species should be approached with caution, given the variable responses observed here across species and functional groups. Moreover, any survey should incorporate location specific fishing knowledge, as an indicator species at one location may not serve as an indicator species at another location. Finally, Ra'ui-specific effects (e.g., age, size, and compliance) may be important uncontrolled sources of variation in this study; these will be examined in Chapter 5.

CHAPTER 4: Spatial variation in size-structure of key resource species as an indicator of Ra’ui effectiveness

ABSTRACT

In general, the size of organisms within marine protected areas (MPAs) is expected to increase. In this chapter I test whether the maximum and mean sizes of common fish and invertebrate species within the lagoon of Rarotonga are significantly greater in Ra’ui than at Control sites. As habitat has been shown to influence the size of fish, I incorporate variation in substrate between Ra’ui and Control sites into the analyses of size distributions (represented by 25th, 50th, 75th and 95th percentiles along a size frequency distribution) for five ubiquitous fish species using permutational multivariate analysis of variance (PERMANOVA). Further, using Manly’s alpha for juveniles and adults of these same five fish species, I assess whether each ontogenetic stage i.e., juveniles or adults, uses habitat differently, and then determine whether the proportion of preferred substrate locally available shapes juvenile and adult densities. Results indicate only one fish species (*Siganus argenteus*) had significantly greater maximum size in Ra’ui relative to corresponding Control sites, while *Mulloidichthys flavolineatus* and *Stegastes nigricans* were the only fish to exhibit a significantly greater mean size in Ra’ui relative to corresponding Control sites. Two of the lagoon invertebrates (*Echinometra mathaei* and *Tripneustes gratilla*) and three of the reef-crest invertebrates (*Echinothrix diadema*, *Echinometra oblonga*, and *Trochus niloticus*) had significantly greater mean size in Ra’ui relative to corresponding Control sites.

Juveniles of five fish species used habitat differently relative to adults. Densities of *Acanthurus triostegus* juveniles increased linearly with the proportion

of preferred substrate cover (r^2 = 0.44, p= 0.011), whereas densities of adult *A. triostegus* (r^2 = 0.46, p= 0.009) and *Ctenochaetus striatus* (r^2 = 0.43, p= 0.035) increased linearly with the proportion of preferred substrate cover. Although not statistically significant, densities of adult *M. flavolineatus* exhibited a trend of decreasing linearly in both Ra'ui (r^2 = 0.49, p= 0.074) and corresponding Control (r^2 = 0.15, p= 0.448) sites with increasing preferred substrate cover, suggesting a possible effect of protection. However, this result was accompanied by an interaction between protection and substrate that is difficult to interpret. Factors including site-fidelity and the mobility of an organism, the level of fishing pressure in the lagoon, disturbance events, sporadic recruitment, and temporal variation in sampling may explain why so few significant increases in size were observed in Ra'ui relative to corresponding Control sites across a wide range of fish and invertebrate species.

INTRODUCTION

Life-history characteristics such as whether an organism is highly mobile or sedentary, long- or short-lived, reaches maturity quickly or slowly, and how fecund it is, can influence how a species responds to exploitation or protection (Jennings *et al.* 1999). Further, these life-history characteristics evolve together as interrelated traits determined by demographic rates that may depend upon the local environment (Williams 1966, Stearns and Crandall 1984). Fishing has enormous impacts on the demographic environment of harvested species by directly affecting population densities, and decreasing the mean size of targeted species (Rochet 1998). The demographic environment created via the removal of older and larger fish results in changes to the age and size structure of fished populations (Jennings and Polunin 1996a, Goni 1998), and exploited fish stocks may respond directly to fishing- induced decreases in population density with increased growth (Stearns and Crandall 1984). Conversely, when fishing levels are reduced or fishing ceases altogether, the mean size and age of the previously fished population may increase (Edgar and Barrett 1999, Sanchez-Lizaso *et al.* 2000, Ashworth *et al.* 2004).

Maximum observed size, an easily measured life-history parameter, has been found to correspond with population trends of harvested fish on coral reefs (Jennings *et al.* 1999) and is a good predictor for other life-history parameters, such as age at maturity (Blueweiss *et al.* 1978). Jennings *et al.* (1999) suggest that the theoretical maximum size (L_∞), which is closely correlated with observed maximum size, may serve as a proxy to indicate the response of a species to fishing. The ease with which observed maximum size can be estimated (for example, via underwater visual census) is of particular relevance in assessing the vulnerability of coral reef fisheries, which tend to be data deficient (Jennings *et al.* 1999, Johannes 1998, Aswani *et al.* 2007).

Marine protected areas (MPAs) are not only expected to increase densities of organisms within their bounds, but also increase the size of targeted fish and invertebrates (Sanchez-Lisazo *et al.* 2000, Westera *et al.* 2003, Begg *et al.* 2005). Although some studies show no increase in mean sizes of fish in MPAs (e.g. Wantiez *et al.* 1997), many other studies have demonstrated an increase in mean size of fish and invertebrates when fishing ceases (see Dugan and Davis 1993 for a review, Buxton and Smale 1989, Edgar and Barrett 1999, Uthicke and Benzie 2000, Ashworth *et al.* 2004, Floeter *et al.* 2006). A recent meta-analysis supports the association of larger sized fish (but not invertebrates) within MPAs (Halpern 2003).

To date, empirical evidence for increased organism size in MPAs remains equivocal, as no studies have incorporated a range of necessary protocols (including Before-After Control-Impact Paired-Series (BACIPS) assessment design, and factoring out confounding effects of habitat) into the assessment of MPA effects (Russ 2002). Further, the claims of meta-analyses remain questionable, as these are based on studies that are potentially systematically confounded (Edgar *et al.* 2004, see Chapter 2 of this thesis for further discussion).

Environmental heterogeneity is one factor known to confound MPA assessments. Although environmental heterogeneity is known to account for variation in fish abundance and diversity, little consideration has been given to its potential to confound assessments of the effects of MPAs (see Chapter Two for further discussion). Further, few studies have looked at how the effects of habitat on the size of fish or invertebrates may confound the effects of MPAs (Jennings *et al.* 1996b, Chapman and Kramer 1999, Chateaux and Wantiez 2005). Of the studies that have controlled for habitat correlates when examining the effects of MPAs on organism size, one study found that 14 of the 26 observed fish species had a significant linear relationship between mean length and one or more habitat variables (Chapman and Kramer 1999). However, another study has suggested no link between habitat and fish and invertebrate size (Hawkins *et al.* 2006). One objective of my study is to assess whether habitat contributes to differences in size between Ra'ui and corresponding Control sites for a number of commonly occurring fish species.

Habitat has also been shown to influence post-settlement processes such as growth and survival for reef fish, with a number of studies demonstrating or suggesting different growth rates that are habitat dependent (Jones 1988, Gust *et al.* 2001). These studies are concordant with the assumption that growth rates are indicative of habitat quality with higher growth indicating better quality habitat e.g., better food supply, suitable shelter from predators (Searcy *et al.* 2007). Hence, if the siting of MPAs is on the basis of good quality habitat relative to other potential sites, then it is likely that if growth of fish and invertebrates will be enhanced, confounding MPA effects with the effects of habitat quality.

In addition to the potential for habitat to influence the size of fish and invertebrates, habitat may also be one determinant of juvenile (small fish) and adult (large fish) fish abundances. Spatial and temporal variation may also contribute to differences observed in the size structure of populations as a number of reef fish undergo ontogenetic shifts in habitat use over their life-cycles (Lecchini and Galzin 2005). Certain habitats may better support different periods in the life-history of an individual (for example, juveniles versus adults), with ontogenetic shifts in habitat use known to occur in many fish species (Gillanders *et al.* 2003, Lechhini and Galzin 2005, Gratwicke *et al.* 2006, Shepherd and Brook 2007). For example, movement of the Nassau grouper, *Epinephelus striatus*, occurs from shallow macroalgal meadows as juveniles to offshore coral reefs as adults (Dahlgren and Eggelston 2001). Niche shifts over the ontogeny of invertebrates are less well known. One example is the Queen Conch, *Strombus gigas*, moving from shallow sand and seagrass habitats to deeper seagrass, sand and algal habitats as it transitions from juvenile to adult (Gillanders *et al.* 2003).

The recognition of crucial links between habitat and the ontogeny of a species is vital. If an MPA is intended to completely protect a species, then all habitats used by that species over its life-cycle needs to be encompassed (PISCO 2007). Here I explore the issue of ontogenetic shifts by examining whether habitat plays a role in association with Ra'ui in determining abundances of juveniles and adults for a number of locally common fish species.

In Chapters 2 and 3 I demonstrated the importance of decoupling the effects of protection from any effects of environmental heterogeneity (e.g., habitat quality, substrate variability) on fish and invertebrate size. Accordingly, here I explore whether size structure differs between Ra'ui and Control sites when the confounding effect of substrate is factored out in my data analysis for a select number of fish species. In this chapter, I address the following questions: (1) Island-wide, do potentially harvested species have a greater maximum size, and greater mean size in Ra'ui relative to corresponding Control sites? (2) Is there evidence that Ra'ui increase the size of some of the more commonly occurring fish species when substrate heterogeneity among sites is factored out in data analysis? (3) Is there a relationship between the proportion of life-stage-specific preferred substrate and i) juvenile, and ii) adult densities for five of the most common fish species, and a concurrent effect of Ra'ui?

METHODS

Sampling regime

Fieldwork was carried out following sampling methods detailed in Chapter 2 and 3. In addition, standard lengths for all diurnal fish species (as per English *et al.* 1997), and size for 18 invertebrate species were estimated. This was done concurrently while gathering abundance data. All fish standard lengths were estimated to the nearest centimetre on snorkel using underwater visual census techniques by one observer (the author) only, while invertebrate sizes were measured predominantly by the author, and two additional persons, using a ruler marked in 1cm increments.

Data Analysis

Overall effects of Ra'ui

To assess whether size structure differed overall between Ra'ui and Control sites, data from each of the 6 Ra'ui and 6 Control sites were treated as replicates in this analysis. Only those species where there was size data for both Ra'ui and Control sites across all sites were selected for analysis i.e., the most commonly occurring fish and invertebrate species. This meant that fish data for 15 species were included for analysis (Table 4.1). For invertebrates, those species found on the reef crest were analysed separately from those inhabiting the lagoon. Twelve invertebrate species from the lagoon were included in the analysis of the overall effects of Ra'ui on size (Table 4.2). Invertebrates from only 2 sites (Parliament and Matavera) at the reef crest were surveyed inside and outside the Ra'ui, with a total of 9 invertebrate species from the reef crest included in analyses (Table 4.3).

As not all data met assumptions necessary for parametric tests, I used the non-parametric Wilcoxon-Mann-Whitney U test (Siegel and Castellan 1988) to test the null hypothesis that the maximum size and mean size of fish or invertebrates was not greater at Ra'ui than Control sites. Size-frequency histograms were plotted for each individual fish species and a two sample one-sided Kolmogorov-Smirnov test (KS test) was used to assess the hypothesis that Ra'ui had size distributions skewed towards larger sizes compared with Control sites.

Relationship between habitat and size structure across sites

Substrate has been shown to influence the size and survivorship of fish. In assessment of the effects of Ra'ui on the size structure of commonly occurring fish, I included the proportion of substrate cover at each site as covariates in my analysis to control for possible substrate effects.

Percentiles (25th, 50th, 75th and 95%) of fish standard length were determined from size-frequency data for each of five abundant fish species at each of the 6 Ra'ui and Control sites. Permutational analysis of variance (PERMANOVA;

Anderson 2001, McArdle and Anderson 2001) was applied to the percentile data for each species with arc-sine transformed proportion cover of all substrates present at each site as covariates to test the null hypothesis of no Ra'ui effect on size structure when substrate is considered.

Relationship between habitat and size: juvenile and adult fish

A number of fish and invertebrates are known to undergo ontogenetic shifts in habitat use. Accordingly, substrate availability during particular stages of an individual's life-cycle (for example, the juvenile phase) may contribute to determining abundances of individuals at that stage.

Size-frequency data for five abundant fish species were split into juveniles and adults based on reported size at maturity for each species (Froese and Pauly 2008, see Table 4.4 for source references), to assess whether the proportion of preferred habitat plays a role in determining the abundance and distribution of juveniles and adults. Manly's alpha (see Chapter 2 for a detailed description) was calculated for juveniles and adults of each of the 5 fish species to determine those substrates disproportionately over-used (and assumed here to represent most preferred) by juveniles and adults. The null hypothesis that juveniles and adults of the same species have similar preferences (as indicated by Manly's alpha) was tested by calculating Bray-Curtis distances and running randomisation tests to assess statistical significance (Pledger *et al.* 2007).

The total proportion of substrate preferred by each juvenile and adult species was calculated by summing together all those substrates (out of the 7 available substrates categorised and censused, see Chapter 2) that had Manly's alpha values greater than 0.143 (values above the 0.143 threshold indicate substrate preference). Densities of juveniles and adults at each site were square-root transformed, and the proportion of preferred substrate cover was arcsine transformed to improve homogeneity of variance. Analyses were carried out separately for juveniles and adults of each of the five species. Linear regression was used to assess whether there was a relationship between the proportion of preferred substrate cover and densities of fish, and whether there is a relationship between the proportion of preferred substrate cover separately for Ra'ui and Control sites. Analysis of covariance (ANCOVA) was used to test for an effect of protection (i.e., Ra'ui) on densities of juveniles (and subsequently, adults), with the proportion of preferred substrate between Ra'ui and Control sites as covariates. *Siganus argenteus* was omitted from the analysis of adults as although there were adults at the Ra'ui sites ($n = 8$), there were no adults at Control sites.

RESULTS

Overall effects of Ra'ui

Fish

Of the 15 species selected for analysis, only one, *Mulloidichthys flavolineatus*, had greater mean size in Ra'ui relative to Control sites (Table 4.1). A greater proportion of larger individuals of *M. flavolineatus* and *Stegastes nigricans* were present within Ra'ui sites relative to Control sites (Figures 4.1 and 4.2) (KS-test: *M. flavolineatus,* $D = 0.199$, $p < 0.0001$; *S. nigricans*, $D = 0.239$, $p = 0.024$). Only one fish species, *Siganus argenteus*, had a greater maximum size in Ra'ui relative to Control sites (Table 4.1). There was also some evidence for *Naso unicornis* having greater mean size in Ra'ui relative to Control sites (Table 4.1).

Non-significant size-distributions are presented in Appendix B, Figure 1 for the 19 other fish species. It appears that a greater proportion of larger individuals were present across Control sites than Ra'ui sites for *Acanthurus triostegus*, *Naso lituratus*, *Rhinecanthus aculeatus*, *Stetholjus bandanensis* and *Chlorurus sordidus* (Appendix B, Figure 1).

Table 4.1 Maximum and mean size (cm) (with standard errors) of all fish at Ra'ui (R) and Control (C) sites and results of one-sided Mann-Whitney U test of the null hypothesis that the maximum size and mean size of fish in Ra'ui is not greater than Control.

	Average Maximum Size (cm)		**Maximum Size Standard Error (cm)**		**Test statistic**	**Mann-Whitney U Test P value**	**Mean Size (cm)**		**Mean Size Standard Error (cm)**		**Test statistic**	*Mann-Whitney U Test P value*
Family and Species	**R**	**C**	**R**	**C**	**W**	**R > C**	**R**	**C**	**R**	**C**	**W**	**R > C**
ACANTHURIDAE												
Acanthurus triostegus	16	14	0.58	1.87	23.5	0.205	8	8	0.12	0.26	87921	0.795
Ctenochaetus striatus	11	14	1.98	2.40	13	0.813	6	6	0.05	0.05	392097	1
Naso lituratus	12	14	2.15	3.20	16	0.656	10	10	0.57	0.76	1150	0.091
Naso unicornis	35	25	6.28	4.37	18	0.147	14	10	6.28	4.37	611.5	0.063
BALISTIDAE												
Rhinecanthus aculeatus	18	20	0.67	3.00	6	0.978	7	8	0.41	0.66	8173	0.886
CHAETODONTIDAE												
Chaetodon auriga	15	15	0.89	0.43	18	0.533	9	9	0.44	0.40	4193	0.539
Chaetodon citrinellus	6	6	0.61	0.75	16.5	0.629	6	6	0.24	0.25	361	0.694
LABRIDAE												
Halichoeres trimaculatus	11	12	0.98	0.40	12.5	0.838	6	7	0.10	0.14	25358	1
Stetholjus bandanensis	9	11	0.37	0.87	6	0.982	7	8	0.10	0.17	3715	0.998
Thalassoma lutescens	14	15	2.35	2.01	15	0.713	11	11	0.34	0.29	10114	0.109
Thalassoma purpureum	17	17	1.43	1.52	20.5	0.372	11	13	0.43	0.77	635	0.986
MULLIDAE												
Mulloidichthys flavolineatus	25	20	1.80	3.63	22	0.287	11	9	0.21	0.13	144738	< 0.0001
Parupeneus multifasciatus	15	17	3.31	3.30	14	0.767	8	9	0.38	0.41	5226	0.267
POMACENTRIDAE												
Chrysiptera glauca	7	9	0.24	0.42	6.5	0.962	5	6	0.09	0.10	8089	1
Stegastes albifasciatus	8	10	0.24	0.68	20.5	0.159	5	6	0.09	0.12	4526.5	1
Stegastes nigricans	11	10	0.86	0.81	17	0.389	7	6	0.18	0.27	3796.5	0.043
SCARIDAE												
Chlororus sordidus	12	21	3.50	3.32	7.5	0.961	11	16	0.41	0.40	8123	1
SERRANIDAE												
Epinephelus hexagonatus	28	15	2.94	1.16	19	0.102	14	12	0.41	0.40	86.5	0.093
SIGANIDAE												
Siganus argenteus	16	8	4.01	1.09	28.5	0.043	5	6	0.02	0.01	1190592	1
Siganus spinus	18	24	1.75	3.44	9.5	0.864	6	13	0.18	0.82	2389.5	1
TETRAODONTIDAE												
Canthigaster solandri	7	7	0.67	0.49	13.5	0.655	5	6	0.36	0.17	397	0.994

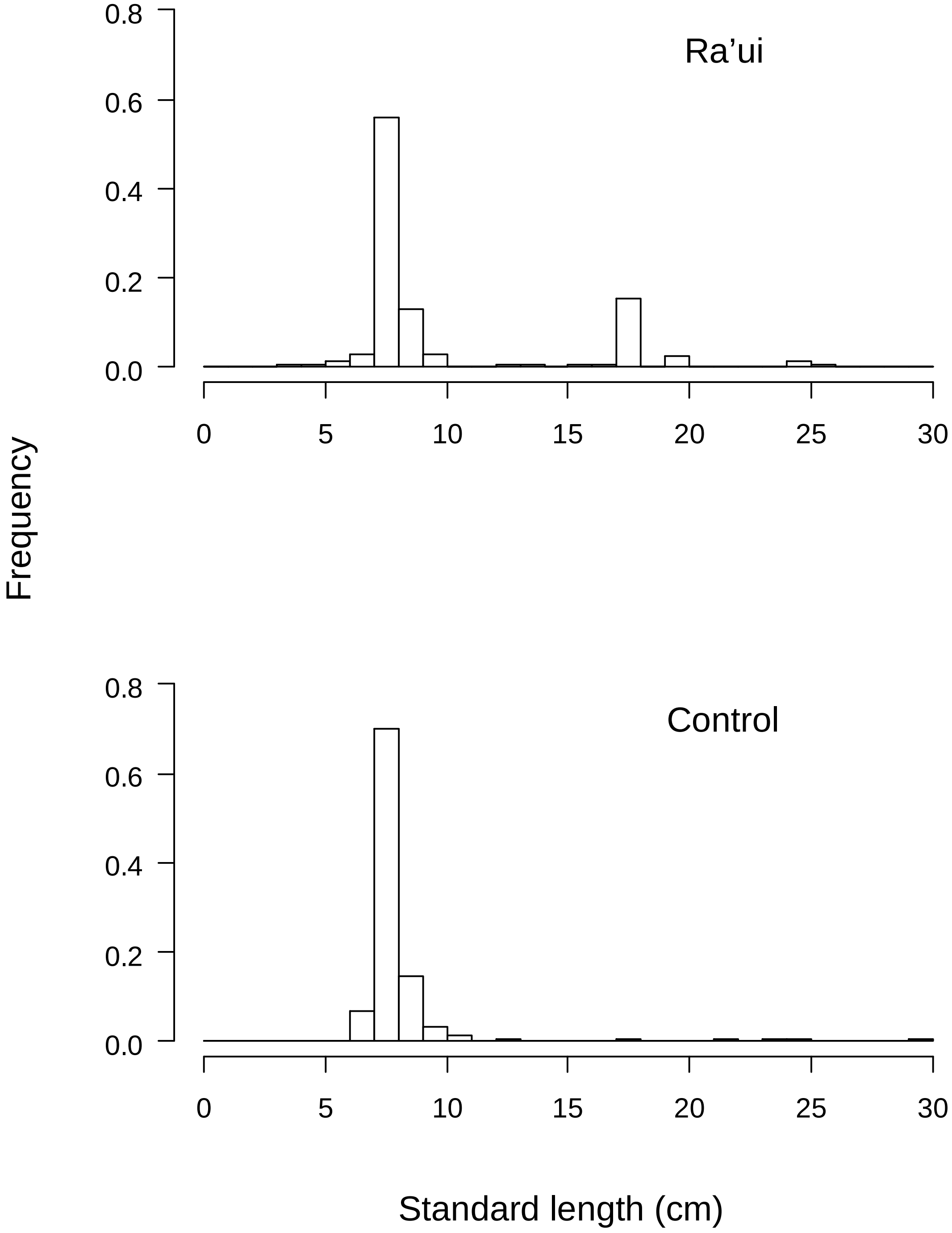


Figure 4.1. Length-frequency distribution for the reef fish, *Mulloidichthys flavolineatus*, across Ra'ui and Control sites.

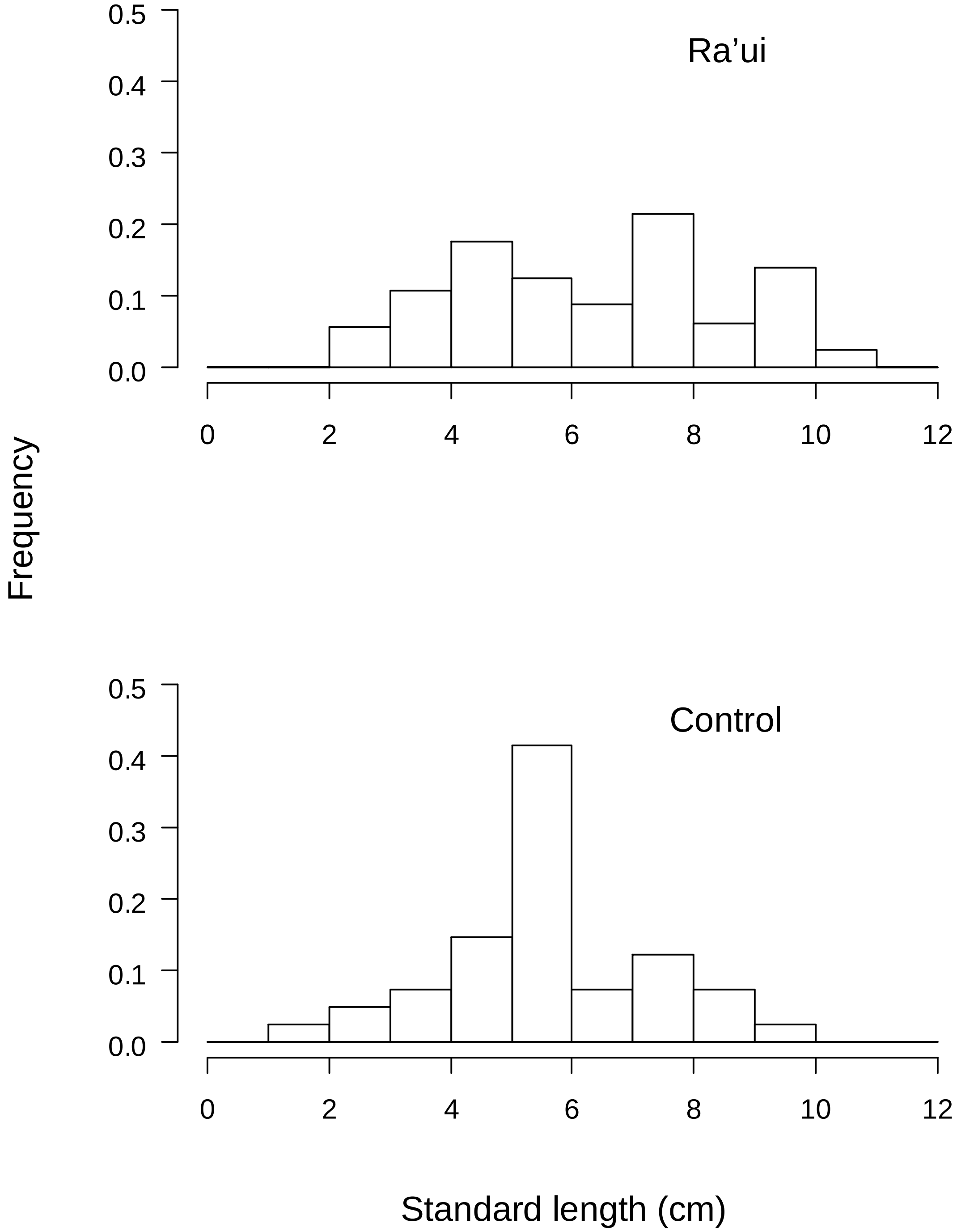


Figure 4.2. Length-frequency distribution for the reef fish, *Stegastes nigricans*, across Ra'ui and Control sites.

Invertebrates

Lagoon

Two of the 12 invertebrate species selected for analysis (the urchins *Echinometra mathaei* and *Tripneustes gratilla*), had greater mean size across Ra'ui relative to Control sites (Table 4.2). Size distributions for *E. mathaei* and *T. gratilla* are presented in Figures 4.3 and 4.4 (KS-test: *E. mathaei,* D = 0.144, $p < 0.0001$; *T. gratilla,* D = 0.278, $p = 0.005$). Size-distributions are presented in Appendix B, Figure 2 for the 10 other lagoon invertebrate species.

Table 4.2 Maximum and mean size (cm) (with standard errors) of all lagoon invertebrates at Ra'ui (R) and Control (C) sites and results of one-sided Mann-Whitney U test of the null hypothesis that the maximum and mean invertebrate size in Ra'ui is not greater than Control.

	Maximum Size (cm)		**Maximum Size Standard Error (cm)**		**Test statistic**	**Mann-Whitney U Test P value**	**Mean Size (cm)**		**Mean Size Standard Error (cm)**		**Test statistic**	***Mann-Whitney U Test P value***
Family and Species	**R**	**C**	**R**	**C**	**W**	**R > C**	**R**	**C**	**R**	**C**	**W**	**R > C**
DIADEMATIDAE												
Diadema savignyi	10	9	0.00	1.11	6	0.587	8	9	0.13	0.37	1041	0.984
Echinothrix diadema	8	7	1.69	1.77	15	0.335	8	7	0.18	0.65	630	0.306
ECHINOMETRIDAE												
Echinometra mathaei	7	7	0.48	0.24	12	0.858	3	3	0.03	0.02	3820731	<0.0001
Echinometra oblonga	3	5	1.44	0.97	3	0.995	2	3	0.85	0.39	50	0.969
TOXOPNEUSTIDAE												
Tripneustes gratilla	9	9	0.98	0.85	7.5	0.771	9	8	0.11	0.19	3810	<0.0001
HOLOTHURIIDAE												
Actinopyga mauritiana	24	18	0.33	8.50	3	0.617	14	17	1.08	4.93	33	0.722
Holothuria atra	31	29	1.11	1.54	26.5	0.097	13	14	0.06	0.06	10531885	1
STICHOPODIDAE												
Stichopus chloronotus	23	24	0.92	1.99	12	0.743	12	14	0.17	0.30	53877	1
OPHIDIASTERIDAE												
Linckia laevigata	31	28	4.58	3.60	8.5	0.440	24	25	1.77	1.23	152	0.825
TRIDACNIDAE												
Tridacna species	12	12	1.25	1.95	19.5	0.436	9	7	0.45	0.49	2314	0.089
TROCHIDAE												
Trochus niloticus	8	7	1.59	1.16	14.5	0.163	4	4	0.09	0.29	4624	0.516
VERMETIDAE												
Dendropoma maxima	2	2	0.24	0.08	16.5	0.146	2	2	0.05	0.06	1523	0.588

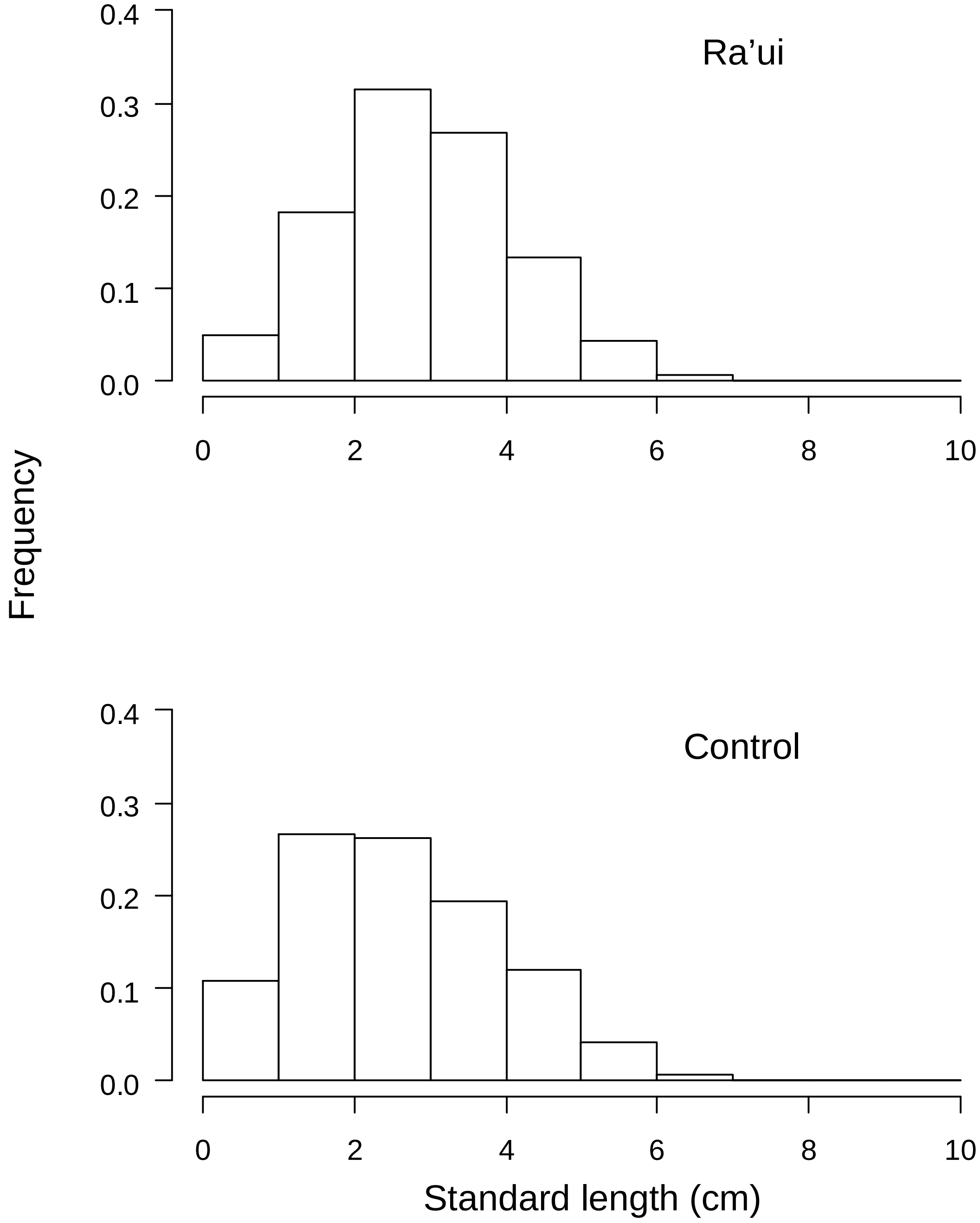


Figure 4.3 Size-frequency distributions for *Echinometra mathaei* across lagoon Ra'ui and Control sites.

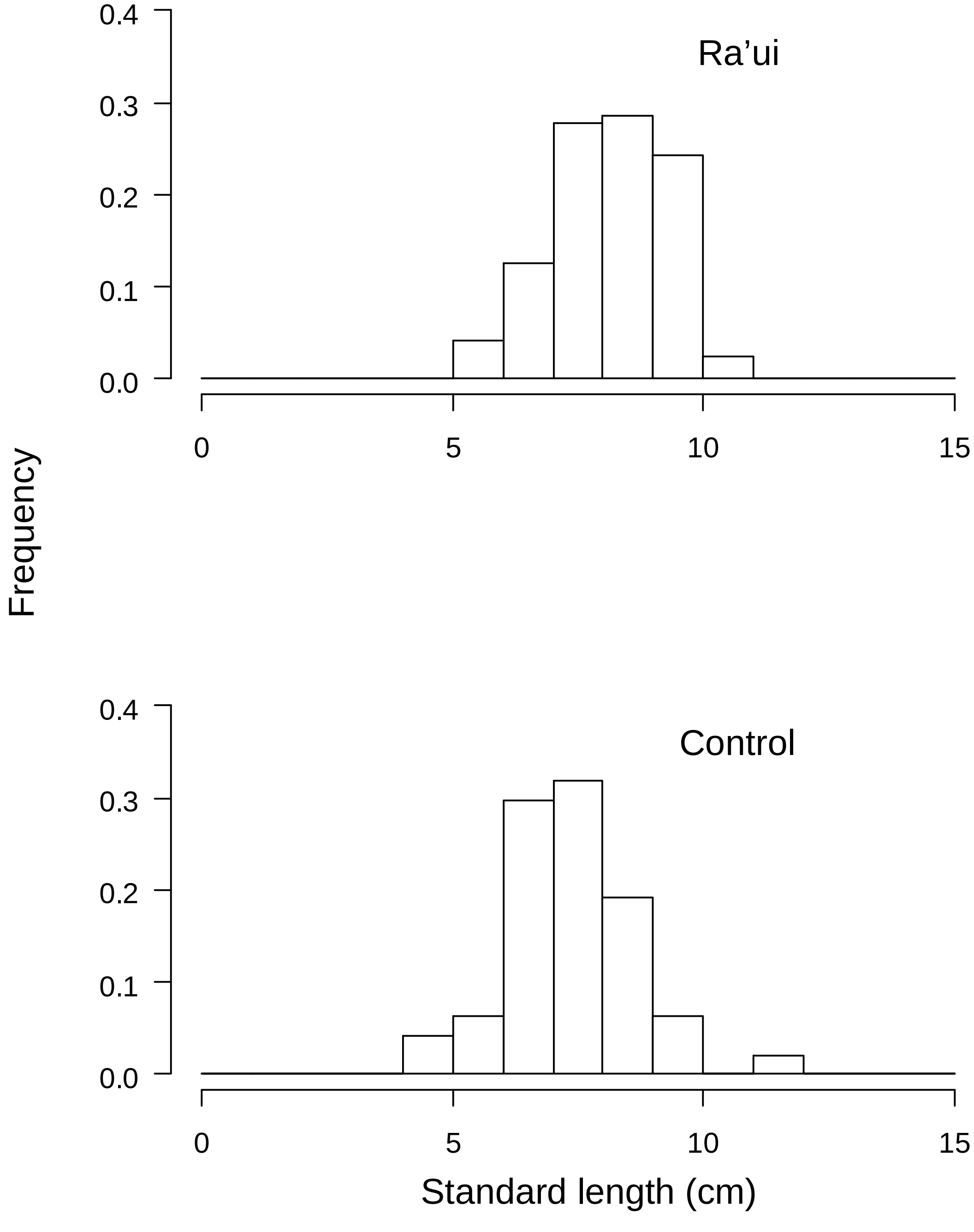


Figure 4.4 Size-frequency distributions for *Tripneustes gratilla* across lagoon Ra'ui and Control sites.

Outer Strata

The urchins, *Echinothrix diadema*, *Echinometra oblonga*, and the gastropod, *Trochus niloticus*, had statistically greater mean sizes in the Ra'ui relative to Control sites (Table 4.3, Figures 4.5, 4.6 and 4.7) (KS-test: *E. diadema,* D = 0.224, $p < 0.0001$; *E. oblonga*, D = 0.361, $p < 0.0001$; *T. niloticus*, D = 0.207, p = 0.005). There was also some evidence for *Holothuria atra* having greater mean size in Ra'ui relative to Control sites (Table 4.3). *Stichopus chloronotus* was not encountered at Ra'ui sites but was present within both sampled Control sites (Table 4.3). Non-significant size-distributions are presented in Appendix B, Figure 3 for the 6 other reef-crest invertebrate species.

Table 4.3 Maximum and mean size (cm) (with standard errors) of all reef crest invertebrates at Ra'ui (R) and Control (C) sites and results of one-sided Mann-Whitney U test of the null hypothesis that the maximum size and mean size of reef crest invertebrates in Ra'ui is not greater than Control.

	Average Maximum Size (cm)		**Mean Size (cm)**		**Mean Size Standard Error (cm)**		**Test statistic**	*Mann-Whitney U Test P value*
Family and Species	**R**	**C**	**R**	**C**	**R**	**C**	**W**	**R > C**
DIADEMATIDAE								
Echinothrix diadema	9	10	7	6	0.07	0.09	63017	<0.0001
ECHINOMETRIDAE								
Echinometra mathaei	5	5	2	3	0.02	0.03	676775	1
Echinometra oblonga	4	3	2	1	0.03	0.03	282863	<0.0001
Heterocentrotus mammillatus	4	3	3	3	0.22	0.30	41	0.734
HOLOTHURIIDAE								
Actinopyga mauritiana	26	25	15	15	0.53	0.56	3250	0.801
Holothuria atra	29	26	16	15	0.49	0.51	8736	0.077
STICHOPODIDAE								
Stichopus chloronotus	-	20	-	9	-	0.50	-	Present in Control only
TROCHIDAE								
Trochus niloticus	12	12	9	9	0.09	0.25	14420	0.036
TURBINIDAE								
Turbo setosus	4	4	3	3	0.14	0.22	261	0.267

Note: To calculate maximum size in the above table, sites were replicates. At the reef-crest I was only able to sample two sites (n = 2). Therefore, standard errors could not be calculated. In addition, the Mann-Whitney U test of the difference between maximum size between Ra'ui and Control could not be carried out.

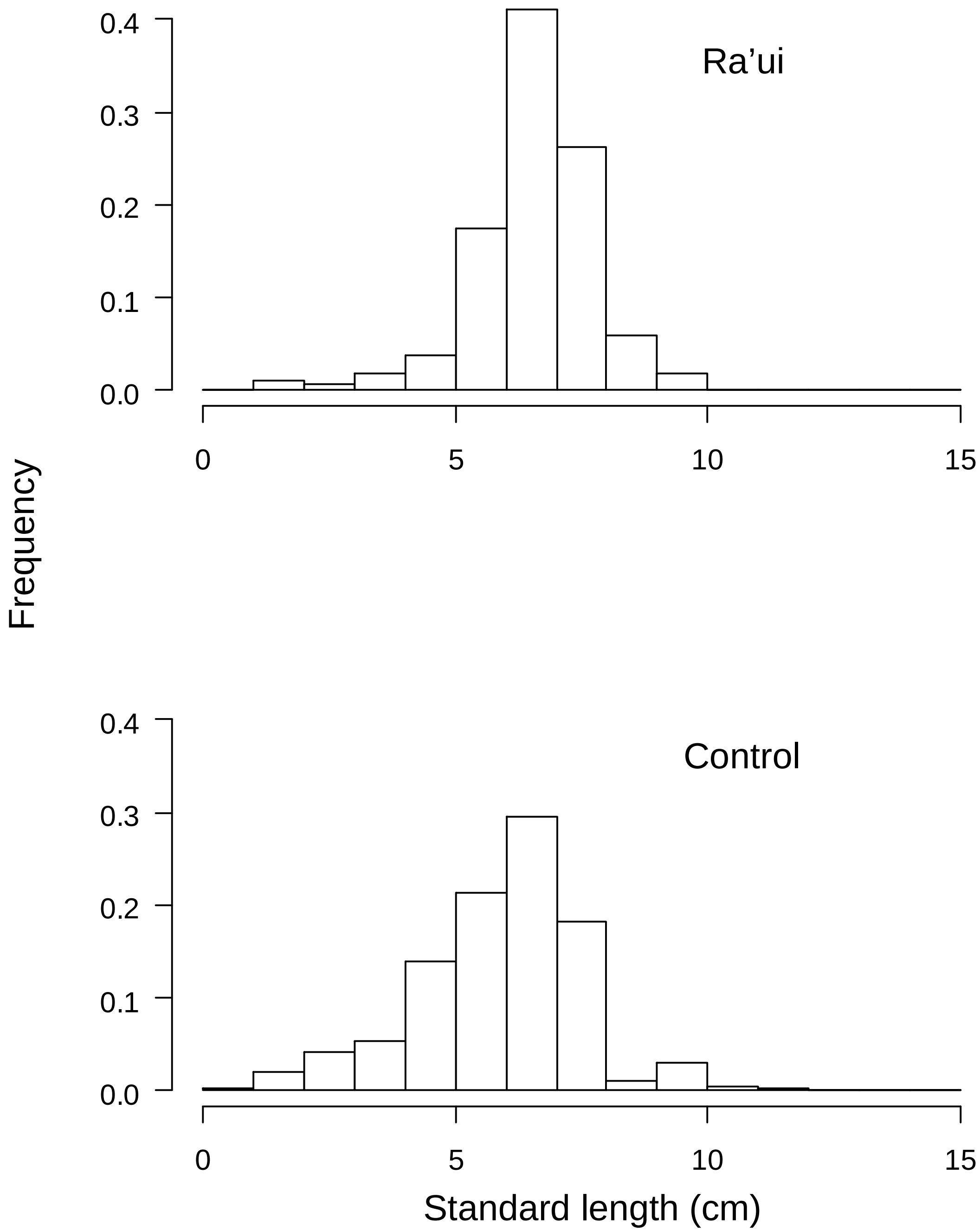


Figure 4.5 Size-frequency distributions for *Echinothrix diadema*, across reef-crest Ra’ui and Control sites.

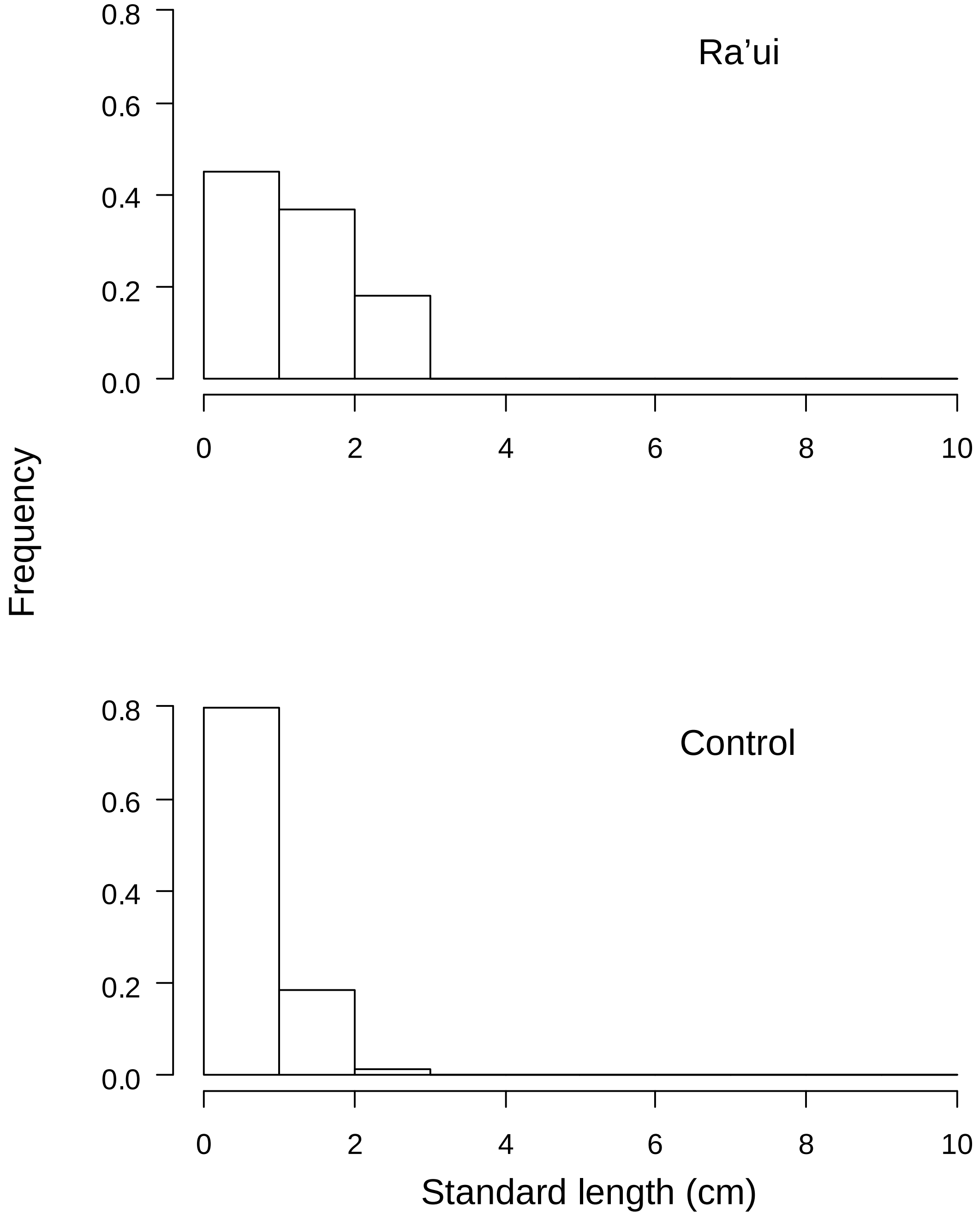


Figure 4.6 Size-frequency distributions for *Echinometra oblonga* across reef-crest Ra'ui and Control sites.

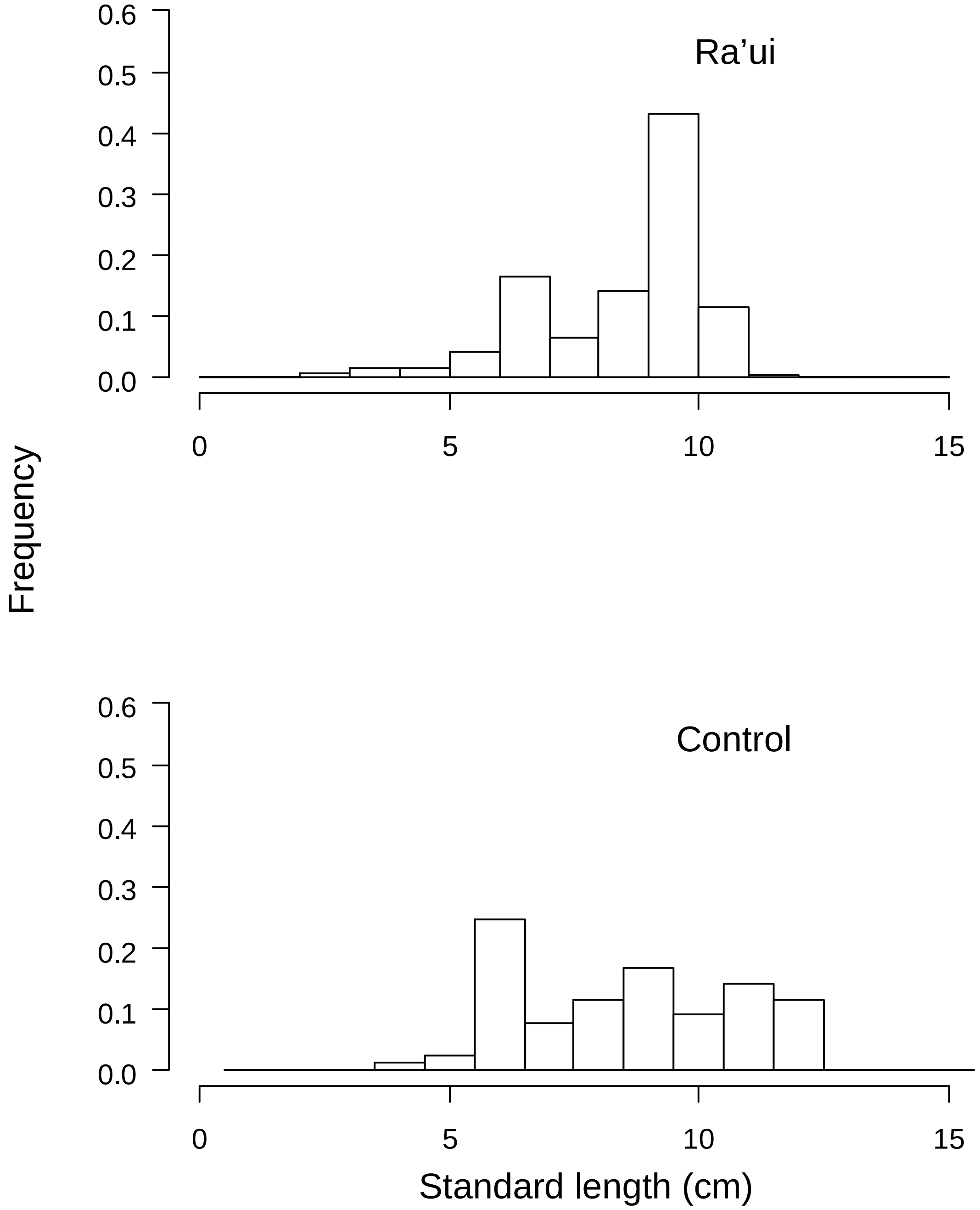


Figure 4.7 Size-frequency distributions for *Trochus niloticus* across reef-crest Ra'ui and Control sites.

Relationship between habitat and size structure across sites

PERMANOVA was carried out with level of protection (i.e., Ra'ui versus Control) as a factor and the proportion of each of the 7 substrate types present at each site as covariates. No significant difference was observed for level of protection on the size-frequency distributions of any of the five common fish species, *Acanthurus triostegus*, *Ctenochaetus striatus*, *Mulloidichthys flavolineatus*, *Chlorurus sordidus*, or *Siganus argenteus*. However, the proportion of substrate cover at each site, was significant in determining the size-distribution of *Acanthurus triostegus* (df = 7, F = 6.5, p = 0.04).

Ontogenetic shifts in habitat use

Based on the information from available literature, size at maturity was estimated for 5 fish species (Table 4.4) and island-wide habitat use was estimated for each species (Figure 4.8). Substrate use was significantly different between juveniles and adults of each species (Figure 4.8). Juvenile *Acanthurus triostegus* mostly used rubble but adults predominantly used dead coral. The other Acanthurid, *Ctenochaetus striatus*, appeared to use both dead and live coral, with adults using dead and live coral but also turf algae (Figure 4.8). Juveniles of *Chlorurus sordidus* mostly used rubble and dead coral with adults largely using dead coral and sand (Figure 4.8). Sand, rubble and pavement were used by juveniles of *Mulloidichthys flavolineatus* with adults using proportionately higher amounts of sand than juveniles. Juveniles of *Siganus argenteus* used a wider range of substrate types (5 substrate types) than adults which used only two substrate types (dead coral and sand) (Figure 4.8).

Table 4.4 Estimated size (standard length (SL)) at maturity of five lagoon reef fish species, with source references.

Scientific Name	Size (SL) at Maturity (cm)	Reference
Acanthurus triostegus	6	Murty 2002
Ctenochaetus striatus	14	Choat and Robertson 2002
Mulloidichthys flavolineatus	11	Myers 1999
Chlorurus sordidus	13	Murty 2002, Gust 2004
Siganus argenteus	20	Myers 1999

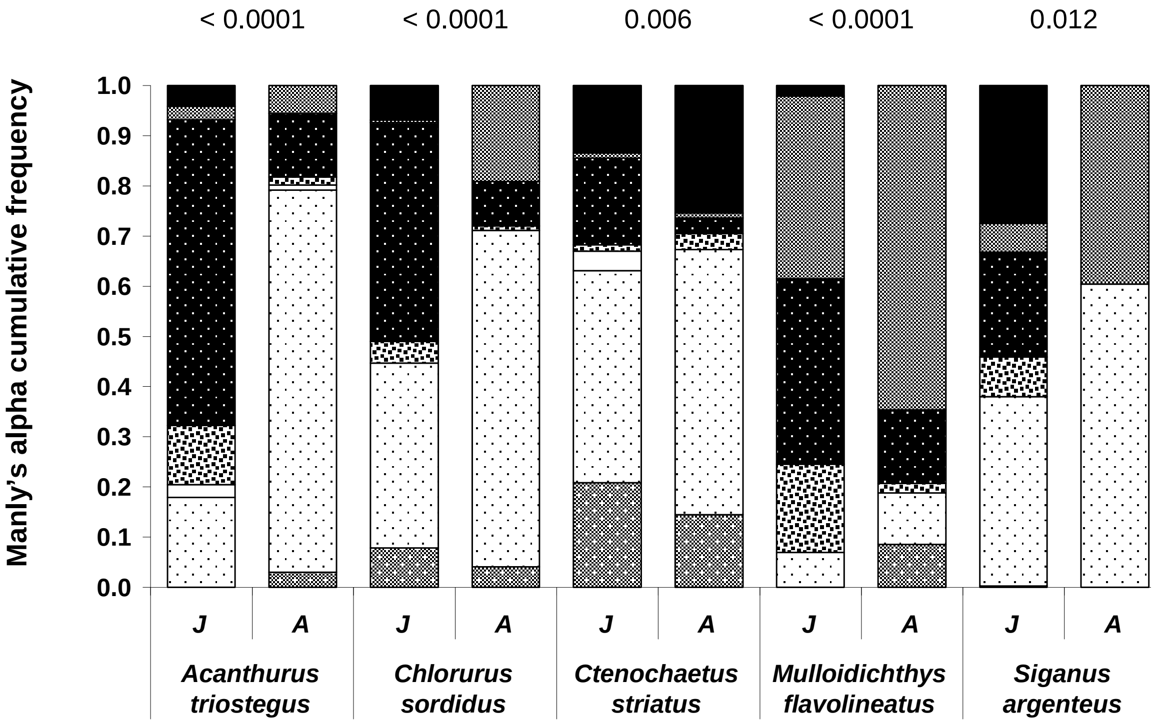


Figure 4.8 Island-wide habitat use indicated by Manly's alpha for juveniles (J) and adults (A) of 5 common lagoon fish species. P-values given above each pair of bars are generated from randomisation tests with values of $p < 0.05$ indicating that juveniles and adults of the same species do not have the same substrate usage. . ■ = turf algae, ▩ = sand, ■ = rubble, ▦ = pavement, □ = other algae, ⬚ = dead coral, ▩ = coral.

Analysis of covariance (ANCOVA) suggested that protection was not significant in determining the abundances of juvenile *Acanthurus triostegus*. However, there was a statistically significant positive relationship between the proportion of preferred substrate cover and the density of juveniles ($y = -2.79 + 8.897(x)$, $n = 12$, $R^2 = 0.44$, $p = 0.011$) (Figure 4.9). Non-significant interaction terms were removed from all ANCOVA models (see Engqvist 2005 for discussion). Protection was significant for *Chlorurus sordidus*, with a significant interaction between protection and substrate but no significant effect of substrate (Ra'ui: $y = 8.632 – 6.637(x)$, $n = 6$, $R^2 = 0.43$, $p = 0.093$; Control: $y = -5.162 + 13.919(x)$, $n = 6$, $R^2 = 0.75$, $p = 0.017$) (Figure 4.9). There was a significant positive relationship between the proportion of preferred substrate cover and densities of juvenile *C. sordidus* in Ra'ui, but this relationship was significantly negative at Control sites. Neither protection nor substrate were significant in determining juvenile abundances for *Ctenochaetus striatus*, *Mulloidichthys flavolineatus*, or *Siganus argenteus* (Figure 4.9).

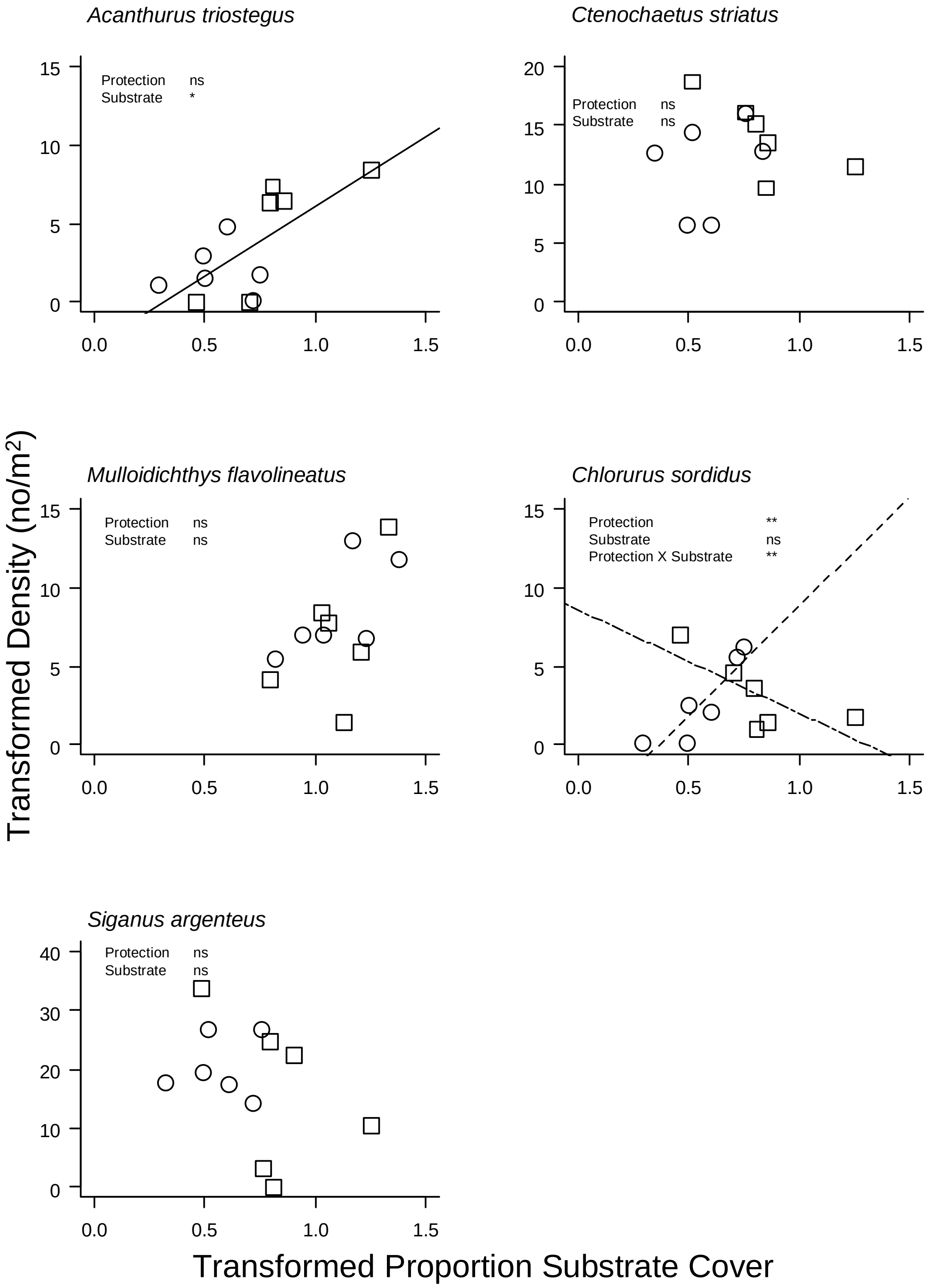


Figure 4.9 The relationship between density (square-root transformed) of juvenile fish and total proportion cover of preferred substrate cover (arcsine transformed) for 5 lagoon fish species for Ra'ui (☐) and Control (○). Results of ANCOVA are displayed on each panel. Where statistically significant, regression lines have been fitted (univariate regression = —, Ra'ui = -----, Control = -—).

ANCOVA suggested that level of protection was not significant in determining adult densities for *Acanthurus triostegus*, or *Ctenochaetus striatus* but there were statistically significant positive relationships between the proportion preferred substrate cover and the density of adults for both fish (*Acanthurus triostegus*: $y = -4.703 + 21.786(x)$, $n = 12$, $R^2 = 0.46$, $p = 0.009$; *Ctenochaetus striatus*: $y = -1.218 + 4.85(x)$, $n = 12$, $R^2 = 0.43$, $p = 0.035$) (Figure 4.10). Protection and substrate were significant in determining adult densities for *Mulloidichthys flavolineatus*. The relationship between the proportion of preferred substrate cover and adult *M. flavolineatus* densities at both Ra'ui and Control sites was negative (Ra'ui: $y = -19.942 + 22.694(x)$, $n = 6$, $R^2 = 0.49$, $p = 0.074$; Control: $y = -2.052 + 3.586(x)$, $n = 6$, $R^2 = 0.15$, $p = 0.448$) (Figure 4.10). There was also a significant interaction between substrate and protection. However, this interaction may be driven by a single site, which if excluded, would likely result in no real pattern. Neither protection nor substrate was significant in determining abundances for *Chlorurus sordidus* adults (Figure 4.10).

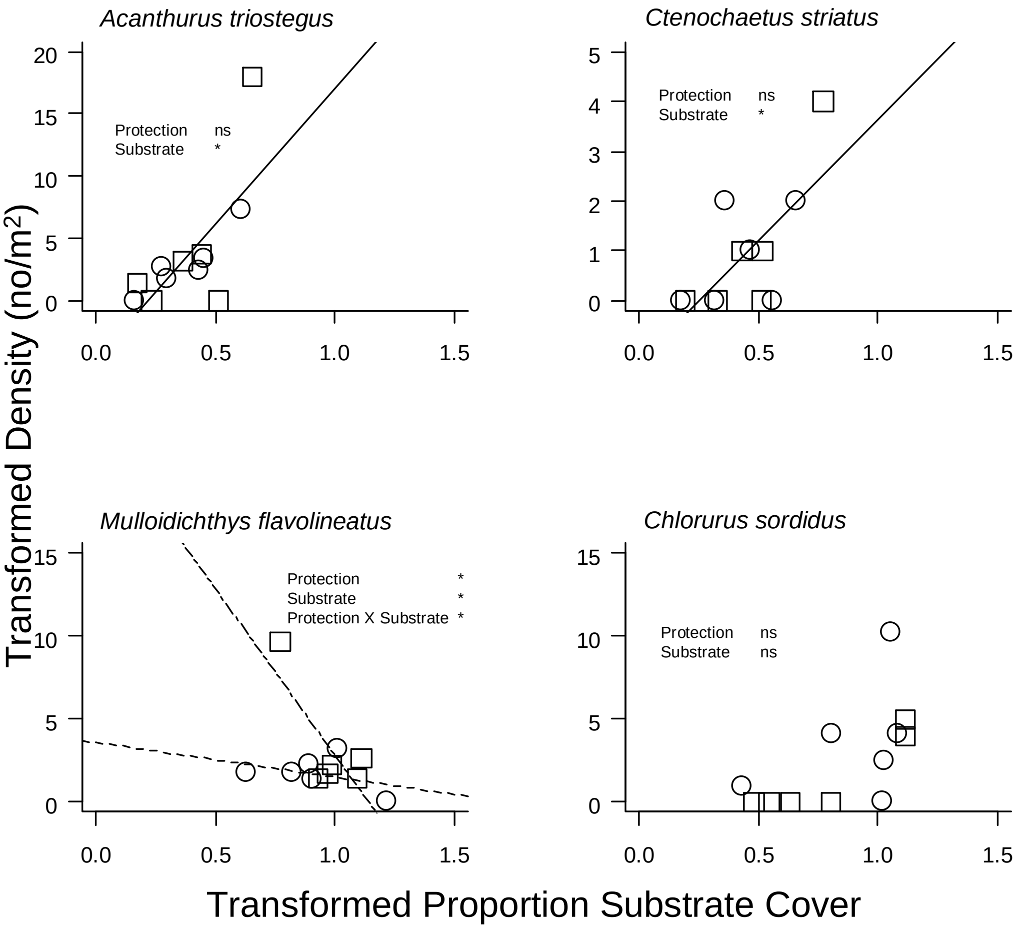


Figure 4.10 The relationship between density (square-root transformed) of adult fish and total proportion cover of preferred substrate (arcsine transformed) for 4 lagoon fish species for Ra'ui (□) and Control (○). ANCOVA results are displayed on each panel. Where statistically significant, regression lines have been fitted (univariate regression = —, Ra'ui = -----, Control = -—).

DISCUSSION

Overall effects of Ra'ui: fish and invertebrates

Siganus argenteus was the only fish species that exhibited greater maximum size across Ra'ui, consistent with my *a priori* expectation of greater maximum size of fish in Ra'ui relative to corresponding Control sites. *S. argenteus* is a food fish (McCormack 2007) that is likely still harvested, and it is possible there is an effect of Ra'ui contributing to its greater maximum size. The size distribution for *S. argenteus* clearly indicated there was a small proportion of larger fish (approximately 20cm standard length) in the Ra'ui that were not present at Control sites (Appendix B, Figure 1). Although *S. argenteus* is a roving herbivore (Diamant 1989) usually seen in small aggregations (Randall 2005), and is likely to easily move between Ra'ui and non-Ra'ui areas, my results provide some evidence supporting harvested fish reaching greater maximum sizes in protected areas.

Across all Ra'ui, only one fish species, the goatfish, *Mulloidichthys flavolineatus*, met my *a priori* expectation of fished species having a significantly greater mean size in the Ra'ui than at Control sites. Site fidelity could be the primary reason why *M. flavolineatus* was the only fish to exhibit greater mean size in Ra'ui. Holland *et al.* (1993) used ultrasonic telemetry to track individual *M. flavolineatus* and found *M. flavolineatus* had strong site fidelity and a restricted home range. Blythe-Skyrme *et al.* (2006) contrasted areas under conventional fisheries management controls with an area under towed-fishing gear restrictions (a form of MPA) and found that fish with low site-fidelity gained few benefits from the MPA. Correspondingly, Malvadkar and Hastings (2008) suggested reserves are appropriate for mobile species if they have at least one of the following qualities; small movement rates, high birth rates to fishing rates, or large habitat sizes. The lack of clear evidence of size increases in the Raúi by the other fish species I examined suggests that these species may have lower site fidelity than *M. flavolineatus*.

Although *M. flavolineatus* is considered to be moderately vulnerable to fishing (Froese and Pauly 2008), previous work has found that the growth rate of *M. flavolineatus* is such that preventing the harvest of the fish for three years would produce a 'marketable product' (i.e., fish standard length ~ 24cm) (Holland *et al.* 1993). *M. flavolineatus* has a relatively short population doubling time of 1.4 – 4.4 years (Froese and Pauly 2008), so it is possible that even with relatively short periods of protection from harvest, effects of protection such as increased size in Ra'ui relative to Control sites may be observed.

Although not statistically significant, there was also some evidence to indicate that *Naso unicornis* may have greater mean size in Ra'ui relative to Control sites. *N. unicornis* is a prized food fish in the Cooks Islands (McCormack 2007), and commonly targeted elsewhere in the Pacific by fishers (Meyer 2003). A tagging study by Meyer and Holland (2005) found that *N. unicornis* were site-attached to home-ranges within the boundaries of a small Hawaiian marine reserve (32 ha). As with *Mulloidichthys flavolineatus*, site fidelity may be why *N. unicornis* mean size was greater in Ra'ui than at Control sites. The Ra'ui on Rarotonga range between 3.3 and 47 hectares, and the size of the Ra'ui (for example Akapuao (35 ha) and Aroko (47 ha), and Aroa (16 ha)) may be adequate to encompass the home-range of *N. lituratus* and provide protection from any fishing.

The other fish species to have a significantly greater mean size in Ra'ui was the highly territorial *Stegastes nigricans*. However, *S. nigricans* is not known to be fished in Rarotonga (it is a small, highly territorial, aggressive damselfish reaching maximum lengths of 13cm standard length (Lieske and Myers 2002, Randall 2005)). A cohort of similar-sized individuals appeared to drive the difference in size distributions between Ra'ui and Control sites for *S. nigricans*. This cohort could be a recruitment pulse signal that has persisted in the Control but not the Ra'ui, with predator / prey interactions one explanation for the reduced size of the cohort in Ra'ui. There were significantly greater numbers of carnivorous fishes in two Ra'ui (Parliament and Tikioki) which may have led to increased predation on juvenile *S. nigricans.*

Two lagoon invertebrates, only one of which is a harvested species (*Tripneustes gratilla*) had significantly greater mean size in Ra'ui relative to Control sites. Three reef-crest invertebrate species, two of which are known to be harvested (*Echinothrix diadema* and *Trochus niloticus*), also had significantly greater mean size within Ra'ui relative to reference sites. Four of the five invertebrate species with greater mean size in the Ra'ui than at corresponding Control sites were echinoderms. The sea cucumber, *Holothuria atra*, also had a trend of increased size in the Ra'ui relative to corresponding Control sites. In comparison to the fish sampled in this study, invertebrates had greater numbers of species exhibiting increased mean size in the Ra'ui relative to Control sites. This result may be due to disparities between the levels of invertebrate harvest and the levels of fish harvested from the lagoon. Invertebrates are still harvested in the lagoon of Rarotonga but rates of harvest for fish may be much lower than invertebrates, especially due to the presence of ciguatera in the lagoon of Rarotonga (Drumm 2004, Moore 2006, SPC 2007, pers. obs.) As already discussed in Chapter 3, if little or no fishing for a species occurs outside Raúi, then there may not be any observed Raúi effect for that species. Results here for invertebrates are also consistent with Parnell *et al.* (2005) who suggest that reserves may be more effective for more sessile or site-attached species (see Chapter Three for brief discussion). Further, the greater mean sizes for three of the invertebrate species at the outer strata may indicate that harvesting of some invertebrate species such as *Trochus niloticus* and the long-spine sea urchin, *Echinothrix diadema,* predominantly occurs on the reef-crest where these species may be easier to access and are found in greater abundances. Other harvested species such as the urchin, *Tripneustes gratilla*, are predominantly found in the lagoon.

The marine gastropod, *Trochus niloticus*, is not generally harvested for food in the Pacific Islands region, however there is a market for its shell (Drumm 2004).

Trocus niloticus had a significantly greater mean size in Ra'ui with this pattern appearing to be driven by a single cohort of similar-sized individuals (90 mm basal area). This cohort could be a recruitment pulse signal that has persisted in Ra'ui but not at Control sites. *T. niloticus* are broadcast spawners and recruitment can be affected due to an allee effect if the parent stock drops below a certain density (Bour 1990). However, as the planktonic phase of *T. niloticus* can last for more than a week, larval *T. niloticus* are likely to be distributed and settle in areas distant from where spawning occurred i.e., both Ra'ui and non-Ra'ui sites. As only two reef-crest sites (Parliament and Matavera) were able to be sampled in this study due to sea conditions, the observed pattern in the size distribution of *T. niloticus* may signal the period since these two Ra'ui were last closed (approximately 4½ to 5 years prior to my surveys), and indicates that Ra'ui are effective for *T. niloticus*.

The sea cucumber, *Stichopus chloronotus*, was only found at Control sites and not Ra'ui on the reef-crest. Lincoln-Smith *et al.* (2006) found that there was no effect of a marine conservation area on the abundance of the sea cucumber, *S. chloronotus*. In addition, the cryptic nature of many juvenile holothurians may decrease the likelihood of detecting increasing size or abundances following implementation of a protected area (Lincoln-Smith *et al.* 2006). It is also possible that predator-prey interactions specific to Ra'ui sites may be occurring on the reef-crest that may be suppressing *S. chloronotus* abundances in Ra'ui, however predation on adult holothurians is thought to be rare (Bakus 1973).

The response of fish and invertebrates to protection can depend on the life-history of the animal, and as a consequence, can vary among species. Perhaps this provides some explanation for my observation of so few statistically significant increases in size for any of the species included in my data analysis. For example, Tuya *et al.* (2006) surveyed two MPAs and found differences in biomass were species-specific across four fished species. Invertebrate species also have differential responses to marine protection. Lincoln-Smith *et al.* (2006) noted that a wide-range of factors such as generation time, degree of prior fishing pressure, and reserve location and size, play a role in the length of time it takes a species to respond to protection from harvest. However, low statistical power may have been the reason I was unable to detect any significant differences in the mean or maximum sizes for many of the fish and inverterbrates between Ra'ui and Control sites. Low statistical power to detect changes in the abundance and size of less common species is one of the disadvantages of underwater visual census of coral reef multispecies assemblages (English *et al.* 1997).

Relationship between habitat and size structure across sites

Substrate heterogeneity may alter interpretations of Ra'ui (and MPA) effects for fish abundances (see Chapter 2 for discussion regarding relationships between fish abundance and habitat). There is also evidence that habitat influences the size structure of fish populations (Jennings *et al.* 1996a, Chapman and Kramer 1999, Chateaux and Wantiez 2005). Yet when I incorporated substrate heterogeneity for five fish species into the analysis of size-frequency distributions (indicated by 25th, 50th, 75th, and 95th percentiles), substrate was significant in determining the size-distribution for only one fish species, *Acanthurus triostegus*. This result could indicate that substrate use may not be as tightly coupled with size as it is with fish densities, and provides some support for not incorporating substrate into the analysis of mean fish and invertebrate size between Ra'ui and Control sites. In addition, habitat on the reef crest did not differ significantly between Ra'ui and Control sites for the reef crest invertebrates (see Chapter 3) so substrate heterogeneity is unlikely to be a confounding factor for the size-structure of the reef-crest invertebrates in my analyses.

My results demonstrating significantly different habitat use between juveniles and adults of each of the five abundant fish species agrees with work showing ontogenetic habitat shifts in temperate and tropical fish (MacPherson 1998, Lecchini and Galzin 2005). Lecchini and Galzin's (2005) work on tropical reef fish in Moorea, French Polynesia, provides evidence of ontogenetic shifts from juvenile to adult habitats occurring for four of the five species I focussed on: *Acanthurus triostegus*, *Chlorurus sordidus*, *Ctenochaetus striatus*, and *Mulloidichthys flavolineatus*. However, Lecchini and Galzin's (2005) work focussed on 'seascapes' which are distinct habitat zones, whereas my work focuses on individual substrate types. This difference in spatial resolution between Lecchini and Galzin's (2005) study and my study makes comparisons of the habitat use of juveniles and adults of each species difficult. However, my results provide some evidence in support of ontogenetic shifts in habitat use occurring between juvenile and adults for some species, and add some weight to the suggestion that habitat supporting all life-history stages for a species, or suite of species, should be incorporated into MPAs (Gillanders *et al.* 2003, PISCO 2007).

I had expected that there would be a relationship between the proportion of preferred substrate cover and juvenile fish densities for both Ra'ui and Control sites. Similarly, I also expected a relationship between the proportion of preferred substrate cover and adult fish densities for Ra'ui and Control sites. However, this relationship only occurred in *Chlorurus sordidus* juveniles in Control sites. Some species exhibited non-significant trends of increasing density with increases in the proportion of preferred substrate. For example, even though protection was not significant in determining *Acanthurus triostegus* densities, the proportion of preferred substrate may play a role in determining densities for this species. These results regarding relationships between the proportion of preferred substrate cover and juvenile fish densities may indicate that proportion of preferred substrate may limit juvenile fish densities for some species.

Of the adult fish, only the goatfish, *Mulloidichthys flavolineatus*, had increased densities with increasing proportion of preferred substrate cover, and only in the Ra'ui. *Acanthurus triostegus* and *Ctenochaetus striatus* densities increased with increasing proportion of preferred substrate cover, but protection was not significant in determining densities. The parrotfish, *Chlorurus sordidus*, showed a non-significant trend towards increased densities with increasing proportion of preferred substrate cover. Again, as with the juvenile fish (and consistent with work associating abundance with habitat types in Chapter 2), the trends observed for three of the adult species in my analysis (increasing density with increasing proportion of preferred substrate cover), may indicate that adult fish may be limited by substrate regardless of protection. My results for substrate use by juvenile and adults add weight to protecting a range of habitat types for all life-history stages.

Level of fishing

I found little evidence for significant increases in mean size and size distributions in Ra'ui. This finding was inconsistent with my expectations of increased size with protection from fishing. Fishing pressure at corresponding Control sites may not be high enough for any Ra'ui effects to be detected, or conversely, there may be non-compliance with Ra'ui. As previously mentioned in Chapter Three, there is scant information about fishing around Rarotonga. However, while fishing in the lagoon still occurs, it is at a level lower than two decades ago (Moore 2006). Fishing occurs primarily for invertebrates rather than fish (Moore 2006, SPC 2007). As such, invertebrates are more likely to exhibit a response to Ra'ui, if compliance with Ra'ui is good (pers. obs, Moore 2006, SPC 2007).

Other factors influencing size

As discussed in Chapter Three, other processes such as trophic interactions may obscure and / or confound MPA effects. Disturbances such as cyclones, which can result in high juvenile mortality and the redistribution of sub-adult fish (Lassig 1983), and recruitment that may vary among sites within years (Williams and Sale 1981) may also influence size structure for some fish and invertebrates around Rarotonga. In addition, temporal variation, including growth of some fish and invertebrates over the sampling period, may have reduced the statistical power to detect patterns of variation in size for fish and invertebrates in my data. This is unlikely however, as sampling of sites / strata was randomised over time to reduce any potential biases arising from sampling over a number of months and tidal cycles.

CONCLUSIONS

Site fidelity of fish and invertebrates appears to play an important role in determining the response of fish and invertebrates to MPAs (Kramer and Chapman 1999). This is evidenced by my observation of increased mean size in Raúi for relatively sessile harvested invertebrates (e.g., *Echinothrix diadema*, *Trochus niloticus,* and *Tripneuestes gratilla*), and a fish with high site fidelity (e.g., *Mulloidichthys flavolineatus*). One important implication of greater body size is the associated higher fecundity of larger individuals and the potential to provide more recruits into the population. Processes other than fishing mortality, such as predation, competition, and recruitment fluctuations (Jones *et al.* 1991, Warner 1991), will also be contributing to the size structure of fish and invertebrate populations. The variability associated with processes such as fluctuations in recruitment makes it difficult to ascertain the effectiveness of MPAs in enhancing the size of fish and invertebrates. In Chapter 5, I will discuss reasons why some Ra'ui appear to be more effective than others in increasing abundance and size of organisms within their boundaries.

CHAPTER 5: Are some Ra'ui more effective than others? Site specific analyses of Ra'ui effects

ABSTRACT

In Chapter 3 I demonstrated that the effects of Ra'ui on fish and invertebrate densities vary in both extent and magnitude. In this Chapter I assess the effectiveness of 6 Ra'ui around Rarotonga using three separate metrics of effectiveness for local assemblages of fish and invertebrates; the proportion of fish and invertebrates exhibiting 1) greater densities, 2) greater mean size, and 3) greater maximum size in Ra'ui relative to corresponding Control sites. The results for individual Ra'ui effectiveness indicate that of the 6 Raúi, Parliament Ra'ui had the highest proportion of fish and invertebrate species with greater densities (0.41), and greater maximum size (0.64) inside Raúi relative to corresponding Control sites while Aroa Ra'ui had the highest proportion of fish and invertebrate species with greater mean size (0.39), relative to corresponding Control sites. Tikioki Ra'ui had the lowest proportion of species with greater densities (0.03) in the Ra'ui, while Aroko and Akapuao Ra'ui had the lowest proportion of species with greater mean size in the Ra'ui (0.00), relative to corresponding Control sites. Akapuao Ra'ui had the lowest proportion of fish and invertebrate species with greater maximum size (0.22) inside Ra'ui relative to corresponding Control sites. I used stepwise backward multiple regressions to assess the influence of Ra'ui characteristics (Ra'ui size (ha), density of fish in Ra'ui, distance from Ra'ui to reef-crest , and the human population in the vicinity of the Ra'ui) as predictors of fish and invertebrate responses to Ra'ui. The effectiveness of Ra'ui in enhancing mean fish and invertebrate size was best predicted by Ra'ui area and total fish density in each Ra'ui (coefficients of both predictor variables were negative, $R^2 = 0.86$,

F = 16.05, p = 0.03). Multiple regressions of Ra'ui characteristics were not significant in predicting the effectiveness of Ra'ui with respect to fish and invertebrate densities or maximum size. I speculate that good compliance due to Ra'ui visibility may explain why some Ra'ui appear to be more effective in enhancing fish and invertebrate densities, mean size, and maximum size, while predator-prey interactions and Ra'ui shape may explain the apparent ineffectiveness of some Ra'ui in enhancing fish and invertebrate densities. Density-dependent effects occurring within Ra'ui and Ra'ui size seem to contribute to variation in putative effects of Ra'ui on mean fish and invertebrate size. These patterns may have important implications for the future design of MPAs.

INTRODUCTION

Increases in density, size, diversity and biomass of fish and invertebrates within MPA boundaries are metrics that have been commonly used to assess the effectiveness of MPAs (Halpern 2003). However, recent meta-analyses of MPA effects and studies of focal MPAs have shown that the effects of protection are not universal, and have concluded that MPA effects vary in both extent and magnitude (Côté *et al*. 2001, Halpern and Warner 2002, Samoilys *et al*. 2007).

In Chapter Three I demonstrated that fish and invertebrate abundances had variable responses to protection across the 6 Ra'ui I surveyed, even when the confounding effects of substrate heterogeneity between Ra'ui and Control sites were factored out in my analyses. The variable responses of fish and invertebrate abundances to Ra'ui from Chapter Three suggest that Ra'ui may also variably affect sizes of fish and invertebrates within them.

Understanding the characteristics of marine protected areas (MPAs) that underpin their effectiveness can assist with future MPA design. However, there is contradictory evidence for the effects of MPA size and age on MPA performance (Côté *et al*. 2001, Halpern and Warner 2003, Claudet *et al*. 2008). In a meta-analysis of the effects of marine reserve characteristics on fish populations, Côté *et al.* (2001) found no correlation between the response to protection in terms of changes in fish abundance and diversity, and any of the reserve characteristics examined (i.e. size, age, latitude of the reserve, and total fish diversity). Halpern (2003) also found that the effects of MPAs on density and biomass were independent of reserve size. However, a more recent meta-analysis found that the response of commercial fish species was dependent on reserve size with a 35% increase in the density of commercial fishes with every 10-fold increase in the size of the no-take zone (Claudet *et al.* 2008).

Accordingly, there may be some characteristics of Ra'ui in Rarotonga that may contribute to some being more effective than others. Characteristics such as the size of the Ra'ui, food supply, level of fishing pressure outside the Ra'ui (see

Chapter Three discussion), and density-dependent effects in the Ra'ui may contribute to Ra'ui effectiveness.

Food supply may contribute to the effectiveness of Ra'ui. Experimental studies have certainly demonstrated that food supply can affect the growth of fish (Jones 1986, Forrester 1990). Further, recent modelling efforts suggest that MPAs should be sited in areas where food is concentrated, for example, upwelling regions (Martell *et al*. 2005). On coral reefs, wave action often moves nutrient-containing waters across barrier reef systems and into downstream lagoons (Glynn 1973, Munro and Williams 1985, Wolanski and Delesalle 1995, Andrefouet *et al*. 2001, Dominici-Arosemena and Wolff 2005, Hamner *et al*. 2007). Consequently, the siting of Ra'ui in areas that receive more nutrients than other areas may contribute to increased growth of organisms. In this study, I use the distance from the shore of the Ra'ui to the reef crest as a proxy for food availability and predictor of Raúi effectiveness. Other studies have found that the level of exposure (e.g., waves) can shape reef assemblages (Friedlander *et al*. 2003, Micheli *et al*. 2005). However, these studies did not discuss the role that exposure plays in moving nutrients across the reef flat into the lagoon.

Total fish density may also contribute to Ra'ui effectiveness, particularly as measured by changes in mean size of organisms. To investigate whether the overall fish density within Ra'ui contributes to Ra'ui effectiveness (e.g., via density-dependent growth mechanisms), I use total fish density (no./m^2) in each Ra'ui as a predictor of Raúi effectiveness. The best established evidence for density-dependent responses in marine organisms is exhibited by growth rates: a large number of studies have demonstrated compensatory density-dependence via increased growth rates of individuals at low densities (see Sanchez-Lisazo *et al.* 2000 for discussion). However, very few studies have attempted to evaluate whether density-dependent changes in life-history traits occur in protected populations, and none have yet demonstrated such changes (Sanchez-Lisazo *et al.* 2000). I assess whether the total density of fish inside Ra'ui contributes to MPA effectiveness, especially in terms of organism size (i.e., density-dependent effects), as reduced growth rates have been reported where fish densities are high (Sanchez-Lisazo *et al.* 2000).

Gerber *et al.* (2002) suggest that fishing pressure outside marine reserves is a key determinant of reserve effectiveness. In any impact assessment, it is difficult to detect impacts with any confidence if the impacts are small relative to natural variability (Osenberg *et al*. 1996). This equally applies to detecting the impacts of MPAs. If levels of fishing outside an MPA are low, then it will be difficult to distinguish an MPA effect from natural variability (Kulbicki *et al*. 2007). Although numerous authors have investigated the influence of fishing intensity on coral reef fish communities, (Russ and Alcala 1998b, Dulvy *et al*. 2004b, Graham *et al*. 2005), to my knowledge, no studies have looked at the effects of a network of MPAs which are sited in areas of differing fishing intensities. Jennings and Polunin (1997) divided the length of the reef fronting qoliqoli (traditional Fijian fishing grounds) by the number of people with fishing rights to assess the effects of fishing on the structure, biomass, and diversity of fish communities. In this study, I use the density of the human population within the vicinity of the Ra'ui as a rough proxy for potential fishing pressure, and as another predictor of Raúi effectiveness.

In this chapter I will focus on densities, mean size, and maximum size of fish and invertebrates at individual Ra'ui sites to assess whether some Ra'ui may be more effective than others in enhancing the abundance and size of fish and invertebrates within their bounds. For each individual Ra'ui site, I calculate response ratios for the mean size of abundant fish and invertebrates. I also assess whether fish and invertebrates had greater maximum sizes in Raúi than in corresponding Control sites. I then use the response ratios for fish and invertebrate size at each Ra'ui, in conjunction with response ratios from Chapter 3 for fish and invertebrate abundances, to assess which Ra'ui appear to be most effective. I assess Ra'ui effectiveness with three separate metrics; the proportion of abundant fish and invertebrates exhibiting 1) increased densities, 2) increased mean size, and 3) increased maximum size in Ra'ui relative to corresponding Control sites.

Finally, I explore the influence of Ra'ui characteristics (Ra'ui size (ha), total density of fish in Ra'ui, distance from Ra'ui to reef-crest, and the human population in the vicinity of the Ra'ui) in predicting the 3 separate metrics of Ra'ui effectiveness. I hypothesised that all four predictor variables would play a part in determining the effectiveness of Ra'ui for organism densities, and that total fish density in each Ra'ui would contribute to Ra'ui effectiveness for mean and maximum size. The age of the Ra'ui were not included in my analyses as the amount of time since the Raúi were implemented, or last lifted, was similar (between 4.5 and 5 years prior to my surveys).

METHODS

Study System and Sampling Regime

Fieldwork was carried out in the lagoon around Rarotonga following sampling methods detailed in Chapters 2 and 3 for the estimation of fish and invertebrate abundances and Chapter 4 for the estimation of fish and invertebrate size.

Data analysis

1). Site specific Ra'ui effects on mean and maximum size of fish and invertebrates

In this chapter I limit my consideration to fish and invertebrate species sizes where the data is sufficient to facilitate separate statistical analyses for each Ra'ui and Control pair. Hence, my data was constrained to five fish species; *Acanthurus triostegus*, *Ctenochaetus striatus*, *Mulloidichthys flavolineatus*, *Chlorurus sordidus* and *Siganus argenteus* (all of which are potentially fished species), 9 lagoon invertebrate species (*Diadema savignyi*, *Echinothrix diadema*, *Echinometra mathaei*, *Holothuria atra*, *Stichopus chloronotus*, *Tripneustes gratilla*, *Tridacna* spp., *Trochus niloticus* and

Dendropoma maxima), and 7 reef crest invertebrate species (*Echinothrix diadema, Echinometra mathaei, Echinometra oblonga, Actinopyga mauritiana, Holothuria atra, Trochus niloticus,* and *Turbo setosus*).

I calculated the mean and maximum size of the above fish and invertebrates for each individual Ra'ui and its corresponding Control site. Where densities for some species at particular sites were too low for analysis, these sites were excluded. Size-frequency histograms for the fish and invertebrates were also plotted for each Ra'ui - Control pair and are contained in Appendix C, Figures 1–3.

Response Ratios for fish and invertebrate mean size

I calculated response ratios (Hedges *et al*. 1999, and see Chapter 2) for the mean size [ln (mean size $_{\text{Ra'ui}}$ / mean size $_{\text{paired Control}}$)] of fish and invertebrates at each site for use in subsequent analyses of relationships with Ra'ui characteristics. Response ratios greater than zero, with confidence intervals that do not overlap zero, indicate a positive response to protection i.e., fish or invertebrates have greater densities, mean, or maximum size inside a Ra'ui than at its corresponding Control site. Values of zero, or less than zero, indicate no response i.e., fish or invertebrates have the same densities, mean, or maximum size within Ra'ui as corresponding Controls, while response ratios less than zero indicate a negative response to Ra'ui i.e., fish or invertebrates have lower densities, mean, or maximum size inside a Ra'ui than at the corresponding Control site. I also calculated 95% confidence intervals for each response ratio based on Hedges *et al.* (1999).

2). *Which Ra'ui are most effective?*

My overall approach estimates Ra'ui 'effectiveness' using local assemblages of fish and invertebrates. I obtain separate estimates of 'effectiveness' for (1) effects on local abundance, (2) mean size, and (3) maximum size. More 'effective' Ra'ui are those with proportionally more species with greater densities, mean, or maximum size relative to corresponding Control sites. Assumptions underlying these measures are considered in the *Discussion*.

Effects on abundance

I used response ratios calculated for lagoon fish and invertebrates (see Chapter Three) as a measure of Ra'ui 'effectiveness', and estimated an overall measure of effectiveness from the proportion of lagoon fish and invertebrates that had significantly greater abundances within Ra'ui boundaries (i.e., positive response ratios – see Chapters Two and Three).

Effects on size

I used response ratios calculated for mean size (see 1. above) as one measure of Ra'ui 'effectiveness'. Whether the maximum size of fish or invertebrates was higher in Ra'ui or corresponding Controls was used as another measure of Ra'ui 'effectiveness'. I estimated an overall measure of effectiveness from the proportion of lagoon fish and invertebrates that had significantly greater mean size, and greater maximum size, within Ra'ui boundaries. As some species were locally rare/absent at particular sites, and were thus not able to be incorporated into size analyses, proportions were based upon the local (i.e. reduced) species pool. Reef crest sites were excluded from the assessment of Ra'ui effects on abundance and size as only 2 Ra'ui sites were sampled on the reef crest, compared with all 6 Ra'ui sites sampled in the lagoon.

3). Possible sources of variation in Ra'ui effectiveness

I carried out 3 separate multiple regressions to examine potential sources of variation that may contribute to each the measures of Ra'ui effectiveness. Dependent variables (i.e. indicators of Ra'ui effectiveness) were the proportion of lagoon fish and invertebrate species out of the total number of species sampled (see table 5.4) having significantly 1) greater densities in Ra'ui; 2) greater mean size in Ra'ui, and 3) greater maximum size in Ra'ui, relative to corresponding Control sites.

Independent Ra'ui characteristics tested in the stepwise multiple regressions included Ra'ui area (ha), distance to reef crest (m), the size of the human population located in the vicinity of each Ra'ui (number of persons), and the total fish density in the Ra'ui (number of fish per m^2). Information regarding Ra'ui size was provided by the Cook Islands Ministry of Marine Resources (Saywood *et al*. 2002, K. Raumea pers comm). The linear distance from the shore of each Ra'ui to the reef crest was estimated by superimposing Ra'ui boundaries onto a georectified coastal aerial photograph mosaic for Rarotonga (Drumm 2004) and linear distance estimated in metres from the centre of the shore within the Ra'ui directly out to the edge of the reef crest. The distance from the shore to the reef crest served as a proxy for food supply to each Ra'ui. Information regarding the human population in the vicinity of the Ra'ui was obtained from the Cook Islands 2006 census (Statistics Office, Cook Islands 2006), which listed the number of persons resident in each of the 12 census districts around Rarotonga, Cook Islands. I extracted data from each census district corresponding with Ra'ui location, using this information as a proxy for potential fishing pressure. Total fish densities within each Ra'ui were calculated as the number of all fish species surveyed within each Ra'ui divided by the total area sampled within each Ra'ui ($100m^2$) giving the density of fish per m^2.

Prior to carrying out the multiple regressions, I calculated partial correlation coefficients in SPSS (SPSS Inc. 2008) while controlling for the effects of each of the dependent variables of Ra'ui effectiveness (density, mean, and maximum size), to assess if there were any correlations between the predictor variables to be included in subsequent multiple regressions. Finally, to assess the influence of Ra'ui characteristics in predicting fish and invertebrate responses to Ra'ui, I used stepwise backward multiple regressions. This analysis was done using the 'step' function in R (R Development Core Team 2006) which utilises

Akaike's information criterion (AIC), penalising any redundant model parameters, and removing the redundant parameters from the model (Crawley 2007). The statistical platform, R, was used for all the above data analyses (R Development Core Team 2006).

RESULTS

Site effects on mean and maximum size of fish and invertebrates

Maximum size and response ratios (with 95% confidence intervals) for mean size were calculated for commonly occurring fish and invertebrates at each Ra'ui site (Table 5.1). Of the six Ra'ui sites, three (Aroa, Parliament, and Matavera) consistently had greater mean size of invertebrates and fish compared to the control site. Three of the five fish species had greater mean sizes in some Ra'ui, but responses were not consistent across all censused Ra'ui. *Ctenochaetus striatus* were found to be larger within Ra'ui at Aroa and Parliament, *Mulloidichthys flavolineatus* were larger within Ra'ui at Aroa, Matavera, Parliament, and Tikioki, and *Siganus argenteus* were larger within Ra'ui at Aroa and Parliament (Table 5.1). Common to all three species, mean size was consistently greater at the Aroa Ra'ui relative to the Control site (Table 5.1). Four of the nine lagoon invertebrate species had significantly greater mean sizes in any of the Ra'ui (*Diadema savignyi* and *Tripneustes gratilla* at Aroa, *Echinometra mathaei* at Matavera, and *Trochus niloticus* at Parliament (Table 5.1). On the reef crest, where only two sites were surveyed, mean size was significantly greater for *Echinothrix diadema, Holothuria atra,* and *Trochus niloticus* at Parliament, *Echinometra mathaei* at Matavera, and *Echinometra oblonga* at Matavera and Parliament (Table 5.1). *Trochus niloticus* was also only present in the Matavera Ra'ui and not in the corresponding Control site (Table 5.1). Size frequency histograms for all fish and invertebrates listed in Table 5.1 are presented in Appendix C, Figures 1 - 3.

Table 5.1 Maximum and mean size (cm) of commonly occurring fish and invertebrates at each Ra'ui (R) and Control (C) site. * indicates that maximum size is greater at Ra'ui sites than corresponding Control sites. Response ratios (RR) with 95% confidence intervals are shown for mean size. * indicates that mean size in the Ra'ui is significantly greater than zero relative to corresponding Control sites as the lower CI is greater than zero. – indicates that a value cannot be calculated (AP = Akapuao, AA = Aroa, AK = Aroko, MT = Matavera, PR = Parliament, TK = Tikioki).

FISH			**Maximum Size (cm)**			**Mean Size (cm)**				**Lower CI > zero?**
Family	**Genus & Species**	**Site**	**R**	**C**	**R > C?**	**R**	**C**	**RR**	**Lower CI (RR)**	
ACANTHURIDAE	*Acanthurus triostegus*	**AP**	15	14	*	9.00	9.34	-0.037	-0.117	
		AA	14	18		6.11	7.22	-0.167	-0.254	
		AK	16	16		5.10	6.72	-0.276	-0.396	
		MT	16	5	*	4.29	3.91	0.091	-0.017	
		PR	17	14	*	5.12	4.87	0.050	-0.085	
		TK	18	16	*	9.86	12.73	-0.255	-0.294	
ACANTHURIDAE	*Ctenochaetus striatus*	**AP**	15	18		5.35	6.07	-0.126	-0.161	
		AA	14	13	*	6.39	5.77	0.103	0.051	*
		AK	7	20		5.02	5.75	-0.136	-0.169	
		MT	6	7		5.34	5.61	-0.049	-0.103	
		PR	7	6	*	5.44	5.15	0.055	-0.000	
		TK	17	17		6.61	6.56	0.008	-0.036	
MULLIDAE	*Mulloidichthys flavolineatus*	**AP**	25	28		8.31	9.25	-0.108	-0.198	
		AA	17	25		12.50	8.90	0.339	0.151	*
		AK	28	18	*	8.79	8.51	0.032	-0.018	
		MT	22	11	*	8.86	8.21	0.077	0.032	*
		PR	29	9	*	9.22	7.93	0.150	0.073	*
		TK	26	30		16.79	9.06	0.617	0.579	*
SCARIDAE	*Chlorurus sordidus*	**AP**	25	30		11.64	17.26	-0.394	-0.443	
		AK	7	18		6.67	12.58	-0.635	-0.736	
		TK	20	24		12.24	20.47	-0.514	-0.578	
SIGANIDAE	*Siganus argenteus*	**AP**	7	13		4.63	6.06	-0.270	-0.289	
		AA	25	7	*	21.00	5.75	1.295	1.232	*
		AK	7	7		5.11	6.00	-0.159	-0.170	
		MT	7	6	*	5.37	5.56	-0.034	-0.065	
		PR	28	6	*	5.57	5.01	0.106	0.086	*
		TK	20	7	*	8.27	5.92	0.334	0.177	*
LAGOON INVERTEBRATES										
DIADEMATIDAE	*Diadema savignyi*	**AA**	10	6	*	7.90	6.00	0.275	0.250	*
	Echinothrix diadema	**AA**	11	10	*	7.75	7.40	0.046	-0.119	
		TK	11	4	*	9.27	4.00	0.840	-	
ECHINOMETRIDAE	*Echinometra mathaei*	**AP**	6	6.5		3.16	4.03	-0.243	-0.291	
		AA	7	8		3.09	3.62	-0.157	-0.190	
		AK	9	6.5	*	3.47	3.63	-0.046	-0.161	
		MT	6	7.5		3.18	2.10	0.413	0.370	*
		PR	7	7		4.13	4.05	0.018	-0.038	
		TK	6	7		3.03	3.90	-0.253	-0.304	

Table 5.1 continued…

LAGOON INVERTEBRATES CONTINUED…			Maximum Size (cm)			Mean Size (cm)				Lower CI > zero?
Family	**Genus & Species**	**Site**	**R**	**C**	**R > C?**	**R**	**C**	**RR**	**Lower CI (RR)**	
HOLOTHURIIDAE	*Holothuria atra*	**AP**	28	35		15.83	17.02	-0.073	-0.173	
		AA	32	25	*	13.54	13.63	-0.007	-0.022	
		AK	35	29	*	12.70	14.44	-0.129	-0.137	
		MT	32	30	*	16.91	15.70	0.074	0.032	
		PR	28	27	*	13.09	15.11	-0.143	-0.155	
		TK	32	25	*	15.08	16.43	-0.086	-0.168	
STICHOPODIDAE	*Stichopus chloronotus*	**AA**	24	25		11.67	13.61	-0.154	-0.179	
		MT	16	26		13.67	19.16	-0.338	-0.475	
		PR	25	20	*	14.17	13.08	0.080	-0.005	
TOXOPNEUSTIDAE	*Tripneustes gratilla*	**AA**	11	10	*	8.75	7.55	0.147	0.098	
TRIDACNIDAE	*Tridacna* **spp.**	**AP**	18	16	*	10.03	9.00	0.108	-0.080	
		AA	14	11	*	6.90	7.00	-0.014	-0.204	
		TK	16	14	*	10.00	8.67	0.143	-0.012	
TROCHIDAE	*Trochus niloticus*	**AA**	6	4.5	*	3.32	3.88	-0.154	-0.419	
		AK	7	11		5.11	7.50	-0.385	-0.660	
		MT	10	6.5	*	3.98	4.65	-0.156	-0.287	
		PR	6.5	4	*	3.80	3.00	0.236	0.093	*
VERMETIDAE	*Dendropoma maxima*	**AP**	2.5	2.5		1.85	1.76	0.047	-0.171	
		AA	2	2		1.63	1.67	-0.022	-0.405	
		TK	3	2	*	2.07	2.00	0.033	-0.092	
REEF CREST INVERTEBRATES										
DIADEMATIDAE	*Echinothrix diadema*	**PR**	10	12		7.09	6.39	0.104	0.076	*
ECHINOMETRIDAE	*Echinometra mathaei*	**MT**	5	5		2.29	1.15	0.693	0.479	*
		PR	5	5		2.01	2.66	-0.282	-0.323	
	Echinometra oblonga	**MT**	4	2	*	1.67	0.70	0.865	0.729	*
		PR	3	3		1.80	1.22	0.386	0.241	*
HOLOTHURIIDAE	*Actinopyga mauritiana*	**MT**	23	25		12.80	15.38	-0.184	-0.286	
		PR	28	25	*	15.63	15.35	0.018	-0.032	
	Holothuria atra	**MT**	32	30	*	15.11	13.47	0.115	0.047	*
		PR	28	27	*	17.29	14.91	0.148	0.087	*
TROCHIDAE	*Trochus niloticus*	**MT**	11	0		8.97	-	-	None present in Control	
		PR	12	12		8.97	8.55	0.049	0.005	*
TURBINIDAE	*Turbo setosus*	**MT**	4	4		2.67	2.33	0.134	-0.133	

Ra'ui effectiveness

Of the 6 Ra'ui, Parliament had the greatest proportion of fish and invertebrate species with higher densities, and maximum size relative to its corresponding Control site while Aroa Ra'ui had the greatest proportion of fish and invertebrate species with greater mean size relative to its corresponding Control site (Table 5.2). Tikioki Ra'ui had the lowest proportion of fish and invertebrate species with higher densities relative to corresponding Control sites, while Aroko and Akapuao Ra'ui had the lowest proportion of fish and invertebrate species with greater mean size in the Ra'ui relative to corresponding Control sites. Akapuao Ra'ui had the lowest proportion of fish and invertebrate species with greater maximum size inside Ra'ui relative to corresponding Control sites (Table 5.2).

Table 5.2 The proportion of lagoon fish and invertebrates per Ra'ui site from Table 5.1 where mean densities, mean size, and maximum size were greater in the Ra'ui (R). The total number of fish and invertebrates in the local species pool for each particular metric and site are in brackets. Note: some species were locally rare/absent at particular sites, and were thus not able to be incorporated into size analyses, so proportions were based upon the local (i.e. reduced) species pool.

	All Fish and Invertebrates		
Site	**Density**	**Mean Size**	**Maximum Size**
Akapuao	0.22 (32)	0.00 (9)	0.22 (9)
Aroa	0.15 (34)	0.39 (13)	0.62 (13)
Aroko	0.06 (34)	0.00 (8)	0.38 (8)
Matavera	0.15 (33)	0.38 (8)	0.54 (8)
Parliament	0.41 (34)	0.38 (8)	0.64 (8)
Tikioki	0.03 (32)	0.22 (9)	0.60 (10)

Sources of variation in Ra'ui effectiveness

The Ra'ui characteristics for use in multiple regressions predicting the response of fish and invertebrate densities and size (mean and maximum size) are presented in Table 5.3. Aroko Ra'ui was the largest Ra'ui in place at the time of my surveys at over 9 times the size of the smallest, Matavera (Table 5.3). Aroko Ra'ui was the Ra'ui located the greatest distance from the reef crest while Matavera Ra'ui was located immediately at the reef crest (Table 5.3). The human population was lowest at Akaoa, in the vicinity of the Aroa Ra'ui, while it was highest at Ngatangiia-Muri, where the Aroko Ra'ui is located (Table 5.3). Total fish densities were highest at Akapuao Ra'ui and lowest at Aroa Ra'ui.

Table 5.3 Ra'ui characteristics included in multiple regressions as predictor variables. For human population, census district is listed in parentheses.

Site	Ra'ui Area (ha)	Distance to reef crest (m)	Human Population (number of persons)	Overall fish density in Ra'ui (number per m^2)
Akapuao	35	642	1645 (Titikaveka)	2.04
Aroa	16	500	955 (Akaoa)	0.70
Aroko	47	785	1815 (Ngatangiia–Muri)	1.59
Matavera	5	143	1490 (Pue-Matavera)	0.91
Parliament	13	429	1373 (Nikao-Panama)	1.38
Tikioki	3.3	671	1645 (Titikaveka)	1.71

There were no significant partial correlations between any of the predictor variables when controlling, separately, for each of the dependent variables of Ra'ui effectiveness (fish and invertebrate density, mean size, and maximum size) (see Appendix C, Table 1). Subsequently, all four predictor variables were retained in the multiple regressions assessing the effectiveness of Ra'ui at enhancing fish and invertebrate densities, mean size, and maximum size.

Stepwise multiple regressions exploring sources of variation in mean organism size retained two of the four Ra'ui characteristics as significant predictors (Table 5.4). The effectiveness of Ra'ui in enhancing mean fish and invertebrate size was best described by Ra'ui area and total fish density in each Ra'ui (Table 5.4). Multiple regressions of Ra'ui characteristics were not significant in predicting the effectiveness of Ra'ui in enhancing fish and invertebrate densities, and maximum size. Regression output generated in R is included in Appendix C, Tables 2 - 4.

Table 5.4 Stepwise backward multiple regression of Ra'ui effectiveness for mean fish and invertebrate size. Predictor variables retained in the regression were Raúi area and total fish density.

Parameter	Beta coefficients	Adjusted R^2	F	P
Ra'ui effectiveness (mean size)		0.86	16.05	0.03
		Partial R^2		
Ra'ui area	-0.0062	0.757		
Total fish density	-0.1997	0.732		

DISCUSSION

Ra'ui 'effectiveness'

My criteria for Ra'ui effectiveness are based on a reduced suite of species where abundances were high enough to allow for separate statistical analyses at each Ra'ui site. Consequently, inferences regarding Ra'ui effectiveness are limited by the reduced dataset which may have excluded potentially important fished species (particularly carnivorous species) such as Serranids and Lutjanids, which were infrequently encountered during my sampling. Based on my criteria for Ra'ui effectiveness, the most 'effective' Ra'ui sites in this study were Parliament Ra'ui for enhancing fish and invertebrate density and maximum size, and Aroa Ra'ui for enhancing fish and invertebrate mean size. The least 'effective' Ra'ui were Tikioki Ra'ui for fish and invertebrate abundances, Aroko and Akapuao Ra'ui for fish and invertebrate mean size, and Akapuao Ra'ui for fish and invertebrate maximum size.

Both Aroa and Parliament Ra'ui are highly visible, which may result in good compliance, and ultimately, greater effectiveness based on my assessment criteria. Drumm (2004), in his assessment of the effects of Ra'ui on reef-top invertebrates on Rarotonga, stated that the very public location of one of the Ra'ui (Nikao), coupled with strong community support for the Ra'ui, ensured good compliance. Aroa Ra'ui is located directly in front of the Rarotongan Beach Resort, with the resort promoting non-extractive use (snorkelling) of the Ra'ui (C Hood, pers comm.), while the Parliament Ra'ui is directly in front of the Cook Islands Parliament buildings. A number of authors have advocated that the effects of non-compliance with MPAs be included in quantitative MPA assessments (Kritzer 2004, Byers and Noonburg 2007). Guidetti *et al.* (2008) looked at the effectiveness of 15 marine reserves in Italy, demonstrating that reserve effectiveness was greatest where enforcement was high. Furthermore, Guidetti *et al.* (2008) noted that in Italy, MPAs are often underfunded and understaffed, which affects the governance of MPAs, and ultimately, MPA effectiveness. Poaching has recently been recognised as a problem in the Matavera Ra'ui, and the traditional leaders have requested that the Ra'ui be legally recognised under the Cook Islands Environment Act 2003 (Tiraa 2006). Subsequently, the varying levels of Ra'ui effectiveness may be due to variable compliance.

Tikioki Ra'ui is the smallest Ra'ui in the lagoon and is long and narrow, covering reef formations that run in a thin strip from the shore out to the reef crest. It is possible that the size and shape of this Ra'ui plays a role in its effectiveness. Kramer and Chapman (1999) predict that reserves with lower edge to area ratios will have higher population densities and mean body sizes. In simulations to assess factors that affect the movement and density of animals in patches of habitat, the edge to area ratio was the main factor that influenced movement in and out of the patch (Buechner 1987). Meester *et al.* (2004) define the ideal shape for MPAs as being m X n rectangles with a configuration of either m = n (square) or m = n+1 (compact rectangle). The long, narrow shape of the Tikioki Ra'ui gives it a high edge to area ratio. The high edge to area ratio allows fish to move easily between Ra'ui and non-Ra'ui areas, thus increasing their vulnerability to being caught. An important implication of high edge to area ratios noted by Buechner

(1987) is that the conservation of threatened species is more difficult, and more so if the species have large home ranges. Consequently, the shape of the Tikioki Ra'ui may make it less effective for fish with large home ranges.

In Chapter Three I noted that Tikioki had a higher abundance of carnivores relative to other fish functional groups. At Tikioki Ra'ui, predator-prey relationships, whereby top predators in the ecosystem may depress local prey densities (Salomon *et al*. 2002), may drive the patterns in abundances for the suite of species I have used to assess Ra'ui effectiveness. Salomon *et al.* (2002) caution that ecological interactions within an MPA may result in declines in prey species, which does not necessarily indicate MPA ineffectiveness. The lower effectiveness of the Tikioki Ra'ui to enhance fish and invertebrate abundances relative to the other Ra'ui in this study may be due to the suite of species I use to assess Ra'ui effectiveness i.e., most are likely prey species with very few being top-predators. This is a limitation of my study driven by a requirement that fish and invertebrate abundances were high enough to allow for separate statistical analyses at each Ra'ui site.

Variation in Ra'ui 'effectiveness'

Ra'ui characteristics (area, distance to reef crest, human population size, and total fish density) included in the multiple regressions here were unable to predict the variability in Ra'ui effectiveness in terms of enhancing mean density or maximum size of fish and invertebrates. It may be that the two proxies I used for food availability and fishing pressure did not adequately represent either of these Raúi characteristics. Although work has been done looking at the effects of exposure (e.g., waves) and MPA status on coral reef fish assemblages (Friedlander *et al.* 2003), none has examined the effect of food availability on MPA effectiveness, where distance to reef crest from the shore of the MPA has acted as a food proxy. Furthermore, sources of primary production on coral reefs include fleshy macrophytes, filamentous algae, and zooxanthellae in coral tissue while detritus and zooplankton carried over the reef via water movement only contributes to a portion of organic production on coral reefs (Lewis 1977). My other proxy for fishing pressure may have been suitable a number of decades ago when fishing on Rarotonga was more widespread, but may be less appropriate as a proxy for fishing pressure now with the decline in fishing on Rarotonga (Moore 2006, see Chapters 3 and 4 for discussion, SPC 2007).

Eighty six percent of the variation in the effectiveness of Ra'ui in enhancing the mean size of fish and invertebrates was explained by Ra'ui area and the total fish density within Ra'ui. This result suggests that higher total fish density may lead to smaller mean sizes of censused fishes and invertebrates within Ra'ui, and it is consistent with suggestions by other workers that the individual growth rate of organisms decreases with increased total fish density at a site (Sanchez-Lisazo *et al.* 2000). Greater mean size of organisms in protected areas is a common measure of MPA effectiveness (Edgar and Barrett 1999, Sanchez Lizaso *et al*. 2000, Halpern 2003, Ashworth *et al*. 2004). Consequently, mean size may not be a good indicator of Ra'ui effectiveness if Ra'ui enhance densities and growth rates are density dependent.

Ra'ui area also contributed to variation in Ra'ui effectiveness for mean fish and invertebrate size, with increasing Ra'ui size leading to a decreased proportion of fish and invertebrates with greater mean size in Ra'ui. In terms of the ideal size for MPAs, modelling studies suggest that for conservation purposes, marine reserves should be as large as practically possible, while for maximising yield for fisheries, reserves should be as small as possible to maximise larval export to areas outside the reserve (Hastings and Botsford 2003). Further, organisms with longer larval dispersal distances need bigger reserves covering a greater proportion of the coastline to maximise persistence of the population under worst-case scenarios (Botsford *et al*. 2003). Kramer and Chapman (1999) predict that densities and mean body sizes of fish will be higher in reserves that (1) cover a greater area (contrary to my result) and (2) have a higher edge to area ratio. Parnell *et al.* (2006)

note that marine reserves should be large enough to sustain those populations that spend the majority of their time in the reserve area. However, my results indicate that the effectiveness of Ra'ui (as measured by mean sizes) may vary inversely with Ra'ui size; this contradicts conclusions of Halpern (2003) and predictions made by Kramer and Chapman (1999).

Halpern (2003) concluded that the relative magnitude of reserve effect was independent of reserve size with even very small reserves having similar magnitude of reserve effects to large reserves. In my study, Ra'ui size ranged from 3.3 to 35 hectares (0.033 to 0.35 km^2). In Halpern's meta-analysis, reserve size ranged between 0.002 and 846 km^2. To assess whether Halpern's meta-analysis covering a wide range of reserve sizes had perhaps masked any relationship for small reserves with reserve area, I extracted Halpern's (2003) data for those reserves that were similar in size (0.002 to 0.0375 km^2) to the Ra'ui. I then regressed Halpern's (2003) reserve size data against the corresponding response ratios for density and biomass (there were no response ratio data for size for the reduced dataset) and, as Halpern found with his complete dataset, there was no significant relationship between reserve area and the magnitude of response. I then removed those reserves in temperate locations from Halpern's (2003) data, leaving only those reserves located in the tropics, and repeated the regression analysis for both the response of density and biomass with reserve size. Again, there were no significant relationships between reserve area and the magnitude of reserve response.

With my data, it is possible that an interaction between the two predictor variables, fish density and Ra'ui size, may contribute to variation in effectiveness of Ra'ui, as measured by mean size. However, in my examination of the partial correlations between predictor variables in the multiple regressions, Ra'ui size was not correlated with total fish density. This implies that if Ra'ui size is not driving the variable patterns in Ra'ui effectiveness for fish and invertebrate mean size, then perhaps some other characteristic that I did not measure may be doing so.

CONCLUSIONS

To summarise, compliance is often neglected as a factor influencing MPA effectiveness (Kritzer 2004, Byers and Noonburg 2007). In Rarotonga, the location (i.e. visibility) and social context (i.e., community support) of Ra'ui likely has some degree of influence on Ra'ui effectiveness. Species interactions (e.g., predator-prey interactions and/or competition for resources) and the physical shape of Ra'ui may also play a role in reducing the effectiveness of Ra'ui on fish and invertebrate densities. My data hint at possible density-dependent effects that may be occurring within Ra'ui, which possibly contribute to variation in certain measures of Ra'ui effectiveness (e.g., as measured by mean sizes). Thus, density dependent growth may confound the use of mean size as an indicator of Ra'ui effectiveness. Contrary to findings of some recent meta-analyses (e.g., Halpern 2003, Claudet *et al.* 2008), I found some evidence that the effectiveness of Ra'ui in Rarotonga may be inversely related to Ra'ui size. Overall, my results highlight variation in potential Ra'ui effectiveness around Rarotonga. This finding, coupled with the identification of characteristics that potentially contribute to Ra'ui effectiveness (Ra'ui area and total fish density), may prove valuable for future Ra'ui assessment and design.

CHAPTER 6: General discussion and conclusions

Overview

The Ra'ui of Rarotonga are a series of relatively small, young, traditionally managed marine protected areas (MPAs). Reef resources within the Ra'ui have been regularly assessed by the Cook Islands Ministry of Marine Resources since the Ra'ui were first implemented (for example Ponia and Raumea 1998, Ponia *et al.* 1998, Raumea *et al.* 2000a, 2000b, Saywood *et al.* 2002). Various researchers have conducted quantitative evaluations of the effectiveness of individual Ra'ui (Manarangi-Trott 2000, Drumm 2004), or characterised the Ra'ui (Cucknell 2005, Egerton 2005, May 2005). The Ra'ui of Rarotonga have also been the subject of interdisciplinary studies focussing on coral reef health (Churcher-Hoffman 2001, Churcher-Hoffman 2002a, 2002b). However, this is the first study of the Ra'ui on Rarotonga that integrates habitat information with abundance and size data in a quantitative evaluation of Ra'ui effects. Further, this study is unique as it examines the effects of a network of temporary closures. In an attempt to generalise MPA effects, this is also the first study of MPA effectiveness to carry out a meta-analysis across a number of sites as part of a single study.

The overall aim of this thesis was to quantitatively evaluate the effects of Ra'ui on fish and invertebrates in the lagoon of Rarotonga. I empirically demonstrated that environmental heterogeneity confounds inferences of Ra'ui effectiveness (generally applicable to MPAs). In agreement with previous studies, I found Ra'ui to be most effective for site-attached organisms, and there was some evidence that habitat availability may limit the abundance of an organism during particular phases of its ontogeny. Contrary to my expectations, density and size response of many organisms to Ra'ui were not consistent and although meta-analyses suggested there was no island-wide effect of Ra'ui, two-factor analysis of covariance suggested island-wide Ra'ui effects for a number of fish and invertebrate species (see Chapter 3). There was also some evidence supporting inverse predator-prey relationships occurring in Ra'ui but this was not consistent across all Ra'ui.

In this chapter I make recommendations based on my key findings from Chapters 2 – 5 for future Ra'ui assessments. Further, some of my recommendations more generally apply to MPA assessments.

Novel framework to remove confounding by environmental heterogeneity

In Chapter 2 I developed a novel framework to confront the problem of environmental heterogeneity confounding the detection of MPA effects. My framework statistically 'removed' the potentially confounding effects of natural environmental variability from my assessment of Ra'ui effects. I recommended that substrate heterogeneity be incorporated into MPA assessment designs confounded by spatial variation (e.g., Control-Impact type assessments) when it is not possible to carry out more robust assessments (e.g., Before-After Control-Impact Paired Series (BACIPS)).

The collection of data to input into the novel framework developed in Chapter 2 is straight-forward, involving only minor modifications to underwater visual census methods using a Control-Impact assessment survey design i.e., habitat use data is collected concurrently with abundance and size data. Although BACIPS survey designs are recommended, Control-Impact survey designs may be more practical in situations where there are neither the resources (funding, personnel), or time (other work has higher priority) to utilise recommended survey designs such as BACIPS. My technique, as with all underwater visual census (UVC) work is restricted by underwater visibility. Although collecting the data for use in this new framework may prove more difficult in high density, multi-species assemblages, it is likely efficient for sampling a select number of indicator species (e.g., Mullidae and Serranidae on coral reefs). Further, my novel framework may even prove useful for BACIPS type assessment designs and strengthen inferences if one component of environmental variation such as substrate heterogeneity can be factored out during data analysis. In the future, a simple computer program could be written to simplify data analysis (i.e., adjusting the data by habitat, then generating response ratios).

Site fidelity, Ra'ui size, and ontogenetic shifts – considerations for the design of MPAs

A number of my findings have important implications for the design of MPAs. In Chapters 3, 4, and 5, a number of my results support suggestions that spatial management (e.g., MPAs) is most effective for organisms with high site fidelity (Hastings and Botsford 1999, Hilborn *et al.* 2004, Botsford 2005, Parnell *et al.* 2005, Blyth-Skyrme *et al.* 2006, Malvadkar and Hastings 2008, see Chapter 1 for discussion). Although the Ra'ui are relatively small protected areas, they appear to have positive effects on the size and abundance of some fish and invertebrates which based on my findings, may be partially attributable to site-fidelity. Further, in Chapter 5 there was a negative relationship between Ra'ui area and the proportion of fish and invertebrates exhibiting greater size in each Ra'ui, contrary to the conclusions of Halpern (2003) and predictions by Kramer and Chapman (1999). In Chapter 4 I noted that the range of habitats within the Ra'ui, and MPAs in general, may limit the abundances of fish at specific stages of their ontogeny. The inclusion of habitats that can support all benthic life-stages of an organism's ontogeny is an important consideration for MPA design.

Tagging studies for some of the key fished species in the lagoon could provide useful information on their movements in the lagoon of Rarotonga that could strengthen any inferences regarding Ra'ui effectiveness. Further, movement patterns of organisms need to be considered when setting up MPAs, as well as when monitoring MPA effectiveness for both coral reef and temperate MPAs. As most species on coral reefs are sessile / site-attached (Hastings and Botsford 1999), MPAs may be highly effective management tools for coral reef fish and invertebrates if factors such as the home-range and habitat use of a species are taken into account in the siting and design of MPAs.

Effectiveness of temporary closures such as Ra'ui

Some authors purport that temporary closures are ineffective for the goal of conserving fish stocks and revitalising fishing grounds. However, there is increasing recognition that community management of marine resources using traditional measures such as periodic reef closures may be more effective due to better community support, than the implementation of large, permanent reserves which may receive little support from communities and consequently have lower compliance (McClanahan *et al.* 2006). In Chapter 1 I suggested that short-lived or rapidly recruiting species might need short or more frequent closures to recover from harvests than longer-lived, slower-growing species. My results in chapter 4 indicate that Ra'ui (due to their ephemeral nature) may be more effective for species with high growth rates (e.g., *Mulloidichthys flavolineatus*). Further, if the target of Ra'ui is species-specific e.g., Ra'ui to prohibit the harvest of *Trochus niloticus*, Ra'ui may still prove effective in conserving and enhancing those stocks.

Community-based marine resource management and Ra'ui effectiveness

Community based marine resource management is common throughout the Pacific region (Johannes 2002, Aswani *et al.* 2007). In Rarotonga, Ra'ui were implemented for a number of reasons including communities noting and becoming concerned about declines in fish and invertebrate stocks (Passfield and Tiraa 1998). Ra'ui are not legally enforced, rather they rely upon social pressures arising from respect for the mana (power) of the traditional leaders for compliance. Drumm (2004) suggests that legal recognition and government support can strengthen village-based authority and marine tenure systems. On the other hand, legislation could erode the mana of the traditional leaders (Tiraa 2006), and further legitimise Western governance frameworks.

If Ra'ui are successful without requiring legislation, one major benefit would be that communities would be aware that they can successfully manage their own marine resources without the need for government intervention which could boost community efforts to protect marine and other natural resources (Passfield and Tiraa 1998). Community support is crucial for the success of MPAs, and impacts on the degree of compliance with an MPA (Johannes 2002, Aswani and Weiant 2004, McClanahan *et al.* 2006).

One limitation of my work is the lack of specific information regarding the level of compliance with Ra'ui and the degree of fishing in surrounding areas. The level of compliance inside MPAs (and fishing pressure outside) can influence MPA effectiveness (see Chapters 3, 4 and 5 for discussion). I suggest that the degree of fishing outside MPAs, and the level of compliance within MPAs needs to be quantified where possible in assessments of MPA effectiveness.

Education and awareness campaigns may help promote community support for MPAs. Over 600 school students attended a highly successful Takitumu lagoon field day held on Rarotonga in June 2008 to raise public awareness regarding the state of the lagoon (Greig 2008). This type of educational activity may help to engender future support for marine management mechanisms such as the Ra'ui on Rarotonga.

Conclusions

This study is unique in its examination of the effects of a network of temporary closures within a single, small lagoon system. The key conclusions of this thesis are that environmental heterogeneity can confound MPA effects, and temporary prohibitions such as Ra'ui may be more effective for some species if certain conditions are met e.g., compliance is good, the target species have high site-fidelity and high population growth rates. Traditional marine management measures such as Ra'ui may also serve important socio-cultural purposes i.e., maintenance or revival of tradition (Johannes 2002), and consequently be better accepted and incorporated by the community. The socio-cultural functions of Ra'ui may engender community support for the conservation and enhancement of lagoon fisheries, which in turn may result in improved Ra'ui effectiveness through better compliance. Finally, this study may provide an important point of comparison for future studies on the Ra'ui in the lagoon surrounding Rarotonga.

APPENDIX A

Table 1. Common names and Cook Islands Māori names for 'abundant' fish and invertebrate species surveyed. Common names and Cook Islands Māori names sourced from McCormack (2007)

Family	**Genus and species**	**Common Name**	**Cook Islands Māori Name**
ACANTHURIDAE	*Acanthurus triostegus*	Convict surgeonfish	Manini
	Ctenochaetus striatus	Striped bristletooth	Maito
	Naso lituratus	Orangespine unicornfish	Ume
	Naso unicornis	Bluespine unicornfish	Ume toro
BALISTIDAE	*Rhinecanthus aculeatus*	Picasso triggerfish	Kōkiri toka
CHAETODONTIDAE	*Chaetodon auriga*	Threadfin butterflyfish	Taputapu rengarenga
	Chaetodon citrinellus	Speckled butterflyfish	Taputapu
LABRIDAE	*Halichoeres trimaculatus*	Threespot wrasse	Pākoukou
	Thalassoma lutescens	Sunset wrasse	Karore
	Thalassoma purpureum	Surge wrasse	Karore
	Stethojulis bandanensis	Redshoulder wrasse	Karore
MULLIDAE	*Mulloidichthys flavolineatus*	Yellowstripe goatfish	Vete
	Parupeneus multifasciatus	Multibarred goatfish	Ka'uru
POMACENTRIDAE	*Chrysiptera glauca*	Grey demoiselle	Katoti
	Stegastes albifasciatus	Whitebar gregory	Katoti
	Stegastes nigricans	Dusky gregory	Katoti
SCARIDAE	*Chlororus sordidus*	Bullethead parrotfish	Pakati
SERRANIDAE	*Epinenephelus hexagonatus*	Hexagon grouper	Pātuki paru
SIGANIDAE	*Siganus argenteus*	Forktail rabbitfish	Mōrava
	Siganus spinus	Scribbled rabbitfish	Maemae
TETRAODONTIDAE	*Canthigaster solandri*	Spotted toby	Ue'ue
INVERTEBRATES			
DIADEMATIDAE	*Diadema savignyi*	Extreme longspine-urchin	Vana
	Echinothrix diadema	Longspine-urchin	Vana
ECHINOMETRIDAE	*Echinometra mathaei*	Pale burrowing-urchin	Kina
	Echinometra oblonga	Black burrowing-urchin	Kinakina
	Heterocentrotus mamillatus	Brown pencil-urchin	Atuke
HOLOTHURIIDAE	*Actinopyga mauritiana*	Surf redfish	Rori puakatoro
	Holothuria atra	Blood sea-cucumber	Rori toto
	Holothuria cinerascens	Flower sea-cucumber	Rori pua
	Holothuria leucospilota	Black soft-spine sea-cucumber	Matu rori
OPHIDIASTERIDAE	*Linckia laevigata*	Vivid-blue starfish	Etu-moana
STICHOPODIDAE	*Stichopus chloronotus*	Greenfish	Rori matie
TOXOPNEUSTIDAE	*Tripneustes gratilla*	Hidden sea-urchin	Avake
TRIDACNIDAE	*Tridacna spp.*	Giant clam	Pa'ua
TROCHIDAE	*Trochus niloticus*	Commercial trochus	Torokāti
TURBINIDAE	*Turbo setosus*	Rough turban	Ariri
VERMETIDAE	*Dendropoma maxima*	Great worm-snail	Ungakoa

Table 2. Categorisation of all fish species sampled in the lagoon around Rarotonga into fine-scale and broad-scale functional groups. KEY: Fine-scale; Pisc = piscivores, C = carnivores, SIF = sessile invertebrate feeders, O = omnivores, MIF = mobile invertebrate feeders, Plankt = planktivores, TH = territorial herbivores, and RH = roving herbivores. Broad-scale; C = carnivores, P/I = planktivore / invertebrate feeders, O = omnivores, H = herbivores.

Family	**Scientific name**	**Common Name**	**Functional Group**	
			Fine-scale	**Broad-scale**
ACANTHURIDAE	*Acanthurus blochii*	Ringtail surgeonfish	RH	H
	Acanthurus leucopareius	Whitebar surgeonfish	RH	H
	Acanthurus nigroris	Bluelined surgeonfish	RH	H
	Acanthurus spp.	Surgeonfish spp.	RH	H
	Acanthurus triostegus	Convict surgeonfish	RH	H
	Acanthurus xanthopterus	Yellowfin surgeonfish	RH	H
	Ctenochaetus flavicauda	Whitetail bristletooth	RH	H
	Ctenochaetus striatus	Striped bristletooth	RH	H
	Naso lituratus	Orangespine unicornfish	RH	H
	Naso unicornis	Bluespine unicornfish	RH	H
	Zebrasoma veliferum	Sailfin tang	RH	H
APOGONIDAE	*Apogon kallopterus*	Iridescent cardinalfish	MIF	P/I
	Apogon nigrofasciatus	Blackstripe cardinalfish	MIF	P/I
	Apogon spp.	Cardinalfish spp.	MIF	P/I
	Cheilodipterus quinquelineatus	Fivelined cardinalfish	C	C
AULOSTOMIDAE	*Aulostomus chinensis*	Trumpetfish	C	C
BALISTIDAE	*Melichthys niger*	Black triggerfish	RH	H
	Rhinecanthus aculeatus	Picasso triggerfish	O	O
	Rhinecanthus rectangulus	Wedge picassofish	O	O
BELONIDAE	*Platybelone argatus platyura*	Keeled needlefish	Pisc	C
BLENNIIDAE	*Blennidae* spp.	Blenny spp.	TH	H
	Istiblennius edentulus	Rippled rockskipper	RH	H
	Istiblennius spp.	Rockskipper spp.	RH	H
	Plagiotremus tapeinosoma	Scale-eating fang blennie	Pisc	C
BOTHIDAE	*Bothus mancus*	Peacock flounder	C	C
CARANGIDAE	*Carangoides ferdau*	Bar jack	C	C
	Caranx melampygus	Bluefin trevally	C	C
CHAETODONTIDAE	*Chaetodon auriga*	Threadfin butterflyfish	O	O
	Chaetodon citrinellus	Speckled butterflyfish	O	O
	Chaetodon ephippium	Saddled butterflyfish	O	O
	Chaetodon lunula	Racoon butterflyfish	O	O
	Chaetodon ornatissimus	Ornate butterflyfish	SIF	P/I
	Chaetodon quadrimaculatus	Fourspot butterflyfish	SIF	P/I
	Chaetodon reticulatus	Reticulated butterflyfish	SIF	P/I
	Chaetodon trifascialis	Chevroned butterflyfish	SIF	P/I
	Chaetodon ulietensis	Pacific double-saddled butterflyfish	O	O
	Chaetodon unimaculatus	Teardrop butterflyfish	O	O
	Chaetodon vagabundus	Vagabond butterflyfish	O	O
	Forcipiger flavissimus	Longnose butterflyfish	C	C
	Heniochus chrysostomus	Pennant bannerfish	SIF	P/I
	Heniochus monoceros	Masked bannerfish	SIF	P/I
DIODONTIDAE	*Diodon hystrix*	Porcupine fish	MIF	P/I
FISTULARIIDAE	*Fistularia commersonii*	Cornetfish	C	C
GOBIIDAE	*Gobiidae* spp.	Goby spp.	SIF	P/I
	Valenciennea strigata	Bluestreak goby	C	C
HEMIRHAMPHIDAE	*Hemiramphidae* spp.	Halfbeak spp.	O	O
HOLOCENTRIDAE	*Holocentrinae* spp.	Squirrelfish spp.	O	O

Table 2 continued. Categorisation of fish sampled in the lagoon around Rarotonga into fine-scale and broad-scale functional groups. KEY: Fine-scale; Pisc = piscivores, C = carnivores, SIF = sessile invertebrate feeders, O = omnivores, MIF = mobile invertebrate feeders, Plankt = planktivores, TH = territorial herbivores, and RH = roving herbivores. Broad-scale; C = carnivores, P/I = planktivore / invertebrate feeders, O = omnivores, H = herbivores.

Family	**Scientific name**	**Common Name**	**Functional Group**	
			Fine-scale	**Broad-scale**
HOLOCENTRIDAE	*Myripristinae* spp.	Soldierfish spp.	Plankt	P/I
	Myripristis berndti	Bigscale soldierfish	Plankt	P/I
	Myripristis chryseres	Yellowfinned soldierfish	Plankt	P/I
	Myripristis kuntee	Pearly soldierfish	Plankt	P/I
	Myripristis woodsii	White-spot soldierfish	Plankt	P/I
	Sargocentron diadema	Crown squirrelfish	C	C
	Sargocentron spiniferum	Long-jawed squirrelfish	C	C
KUHLIIDAE	*Kuhlia mugil*	Barred flagtail	Plankt	P/I
KYPHOSIDAE	*Kyphosus cinerascens*	Topsail drummer	RH	H
LABRIDAE	*Cheilinus chlorourus*	Floral wrasse	MIF	P/I
	Cheilinus trilobatus	Tripletail wrasse	MIF	P/I
	Cheilio inermis	Cigar wrasse	MIF	P/I
	Coris aygula	Clown coris	MIF	P/I
	Gomphosus varius	Bird wrasse	C	C
	Halichoeres hortulanus	Checkerboard wrasse	MIF	P/I
	Halichoeres margaritaceus	Weedy surge wrasse	C	C
	Halichoeres marginatus	Dusky wrasse	MIF	P/I
	Halichoeres trimaculatus	Threespot wrasse	MIF	P/I
	Labridae spp.	Wrasse spp.	C	C
	Labroides bicolor	Bicolour cleaner wrasse	C	C
	Labroides dimidiatus	Bluestreak cleaner wrasse	C	C
	Macropharyngodon meleagris	Leopard wrasse	MIF	P/I
	Novaculichthys taeniourus	Rockmover wrasse	SIF	P/I
	Pseudocheilinus hexataenia	Sixline wrasse	MIF	P/I
	Stethojulis bandanensis	Redshoulder wrasse	MIF	P/I
	Thalassoma hardwicke	Sixbar wrasse	C	C
	Thalassoma lutescens	Sunset wrasse	MIF	P/I
	Thalassoma purpureum	Surge wrasse	C	C
	Thalassoma trilobatum	Christmas wrasse	C	C
LETHRINIDAE	*Gnathodentex aurolineatus*	Yellowspot emperor	MIF	P/I
	Lethrinus atkinsoni	Pacific yellowtail emperor	C	C
	Monotaxis grandoculis	Bigeye bream	MIF	P/I
LUTJANIDAE	*Lutjanus fulvus*	Flametail snapper	C	C
	Lutjanus kasmira	Bluelined snapper	C	C
	Lutjanus monostigma	Onespot snapper	C	C
MUGILIDAE	*Crenimugil crenilabis*	Fringelip mullet	RH	H
	Liza vaigensis	Squaretail mullet	RH	H
MULLIDAE	*Mulloidichthys flavolineatus*	Yellowstripe goatfish	MIF	P/I
	Mulloidichthys vanicolensis	Yellowfin goatfish	MIF	P/I
	Parupeneus barberinus	Dash-and-dot goatfish	MIF	P/I
	Parupeneus bifasciatus	Twobar goatfish	MIF	P/I
	Parupeneus ciliatus	Whiteline goatfish	MIF	P/I
	Parupeneus cyclostomus	Yellowsaddle goatfish	Pisc	C
	Parupeneus multifasciatus	Multibarred goatfish	MIF	P/I
MURAENIDAE	*Echidna nebulosa*	Snowflake moray	C	C
	Gymnothorax javanicus	Giant moray	C	C
	Muraenidae spp.	Moray spp.	C	C

Table 2 continued. Categorisation of fish sampled in the lagoon around Rarotonga into fine-scale and broad-scale functional groups. KEY: Fine-scale; Pisc = piscivores, C = carnivores, SIF = sessile invertebrate feeders, O = omnivores, MIF = mobile invertebrate feeders, Plankt = planktivores, TH = territorial herbivores, and RH = roving herbivores. Broad-scale; C = carnivores, P/I = planktivore / invertebrate feeders, O = omnivores, H = herbivores.

Family	Scientific name	Common Name	Functional Group	
			Fine-scale	**Broad-scale**
OSTRACIIDAE	*Ostracion cubicus*	Yellow boxfish	O	O
PINGUIPEDIDAE	*Parapercis millepunctata*	Blackdotted sandperch	C	C
	Pinguipedidae spp.	Sandperch spp.	C	C
POMACANTHIDAE	*Centropyge flavissimus*	Lemonpeel angelfish	TH	H
	Pomacanthus imperator	Emperor angelfish	O	O
POMACENTRIDAE	*Abudefduf septemfasciatus*	Banded sergeant	O	O
	Abudefduf sexfasciatus	Scissortail sergeant	Plankt	P/I
	Abudefduf sordidus	Blackspot sergeant	TH	H
	Chrysiptera brownriggii	Surge demoiselle	O	O
	Chrysiptera glauca	Grey demoiselle	O	O
POMACENTRIDAE	*Dascyllus aruanus*	Humbug dascyllus	Plankt	P/I
	Plectroglyphidodon imparipennis	Brighteye damsel	SIF	P/I
	Pomacentrus pavo	Blue damsel	O	O
	Pomacentrus vaiuli	Princess damsel	O	O
	Stegastes albifasciatus	Whitebar gregory	TH	H
	Stegastes fasciolatus	Pacific gregory	TH	H
	Stegastes lividus	Bluntsnout gregory	TH	H
	Stegastes nigricans	Dusky gregory	TH	H
	Stegastes spp.	Gregory spp.	TH	H
PRIACANTHIDAE	*Priacanthidae* spp.	Bigeye spp.	Plankt	P/I
SCARIDAE	*Calotomus carolinus*	Stareye parrotfish	RH	H
	Cetoscarus bicolor	Bicolor parrotfish	RH	H
	Chlorurus frontalis	Tanface parrotfish	RH	H
	Chlorurus microrhinos	Pacific steephead parrotfish	RH	H
	Chlorurus sordidus	Bullethead parrotfish	RH	H
	Scaridae spp.	Parrotfish spp.	RH	H
	Scarus altipinnis	Filamentfin parrotfish	RH	H
	Scarus psittacus	Palenose parrotfish	RH	H
	Scarus schlegeli	Schlegel's parrotfish	RH	H
SCORPAENIDAE	*Scorpaenopsis diabolus*	Devil scorpionfish	C	C
SERRANIDAE	*Epinephelinae* spp.	Grouper spp.	C	C
	Epinephelus hexagonatus	Hexagon grouper	C	C
	Epinephelus merra	Honeycomb grouper	C	C
	Epinephelus polyphekadion	Marbled grouper	C	C
	Grammistes sexlineatus	Sixstripe soapfish	C	C
SIGANIDAE	*Siganus argenteus*	Forktail rabbitfish	RH	H
	Siganus spinus	Scribbled rabbitfish	RH	H
SYNGNATHIDAE	*Corythoichthys flavofasciatus*	Network pipefish	Plankt	P/I
TETRAODONTIDAE	*Arothron meleagris*	Guineafowl puffer	MIF	P/I
	Arothron nigropunctatus	Blackspotted puffer	MIF	P/I
	Canthigaster solandri	Spotted toby	O	O
ZANCLIDAE	*Zanclus cornutus*	Moorish idol	O	O

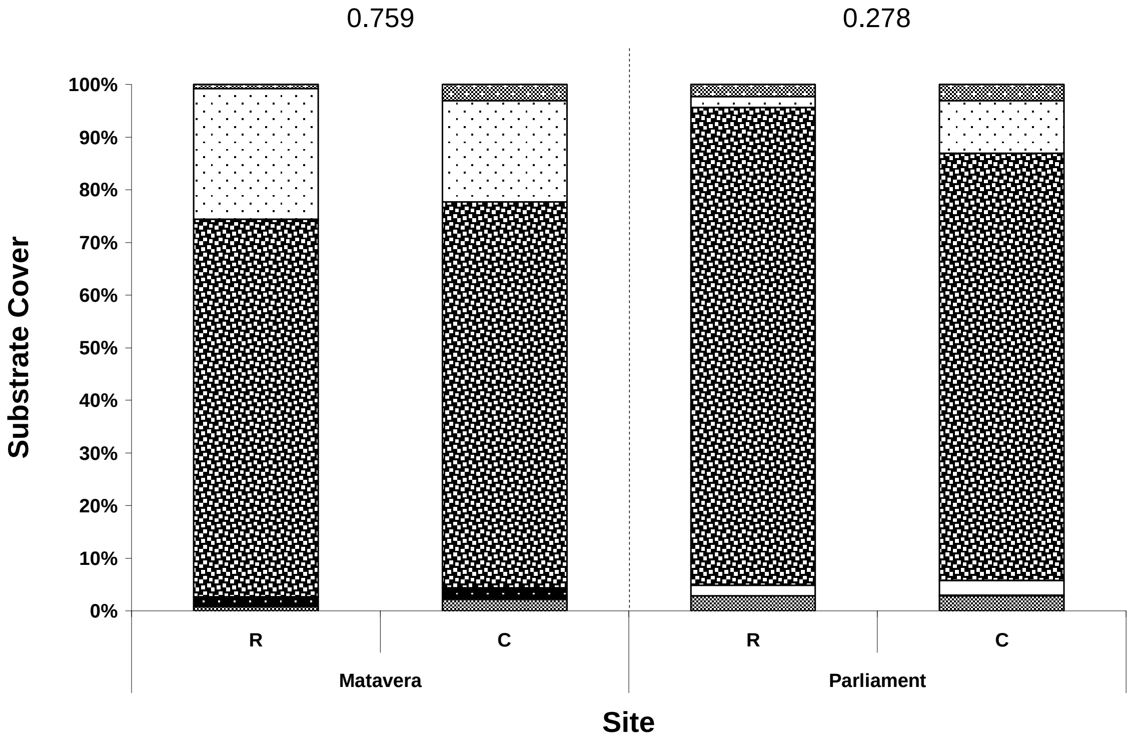


Figure 1. Cumulative percent cover of substrate per reef-crest site by status (Ra'ui and Control). P-values at top of both charts are results from a MANOVA of Arc-sine square-root transformed proportion substrate cover for each Ra'ui and Control pair. C ▩ = live coral, D ⬚ = dead coral, OA ☐ = other algae, P ▩ = pavement, R ■ = rubble, S ▨ = sand.

APPENDIX B

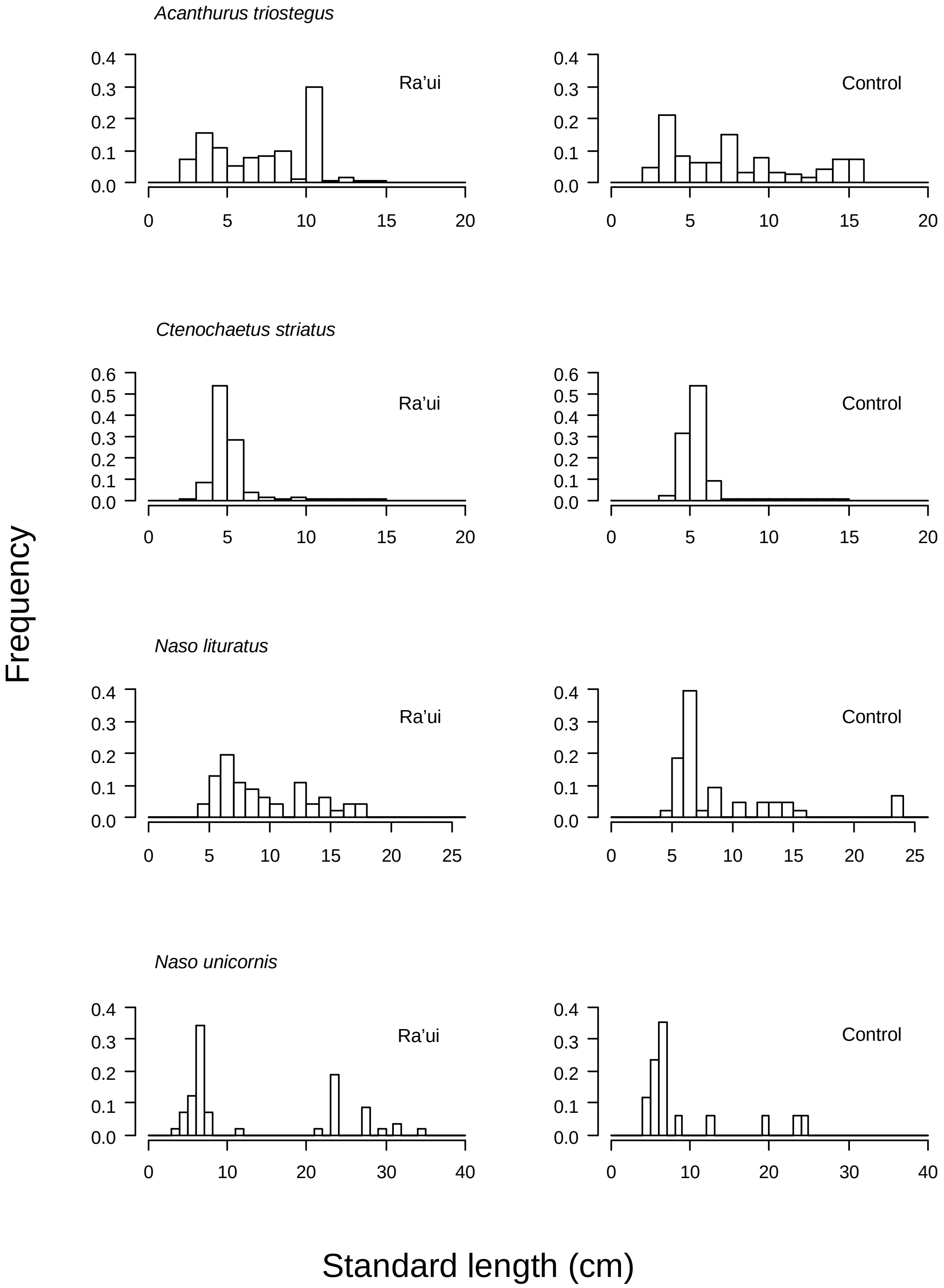


Figure 1. Non-significant length-frequency distributions of each fish species pooled across Ra’ui and Control sites.

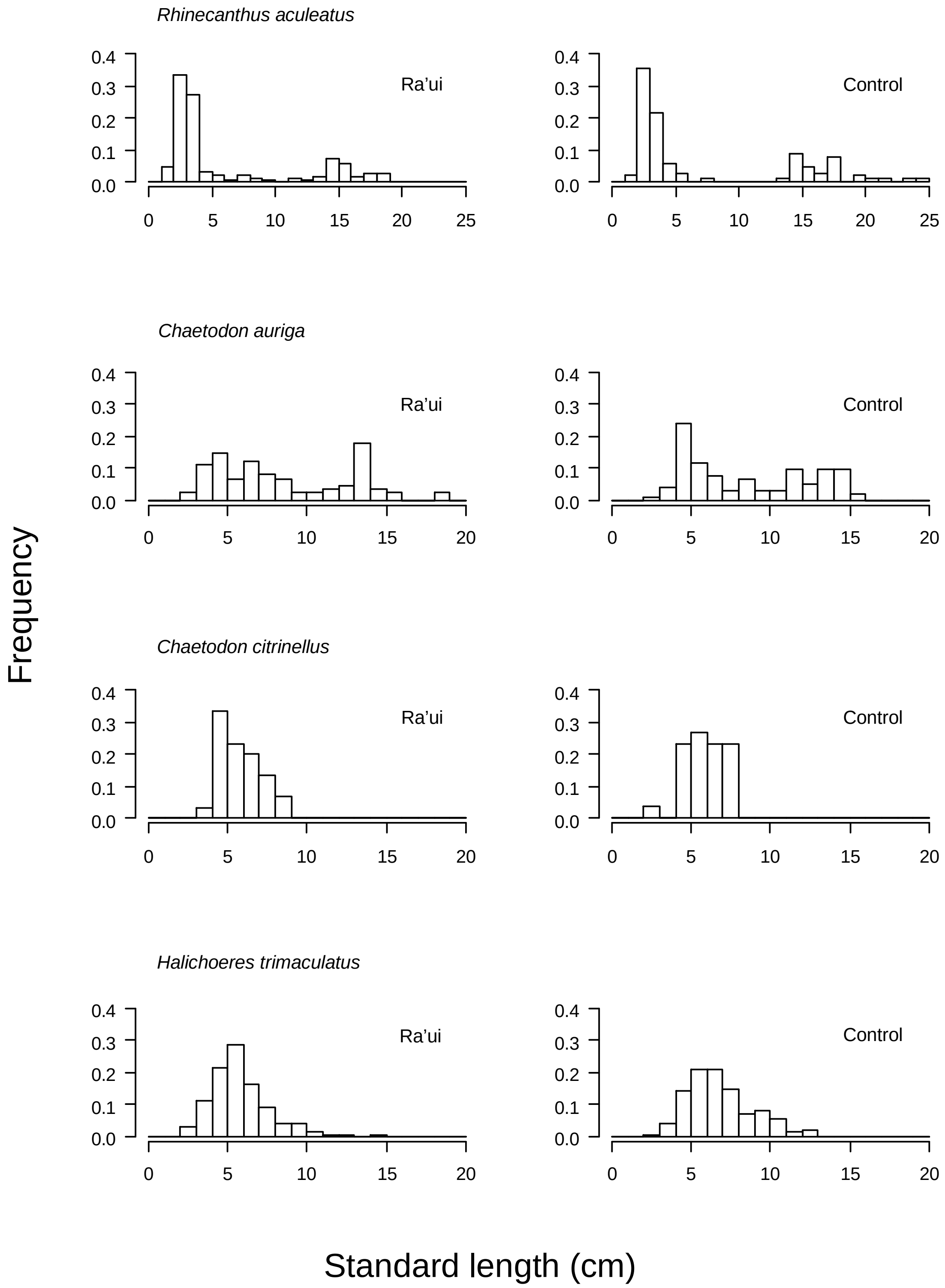


Figure 1 continued. Non-significant length-frequency distributions of each fish species pooled across Ra'ui and Control sites.

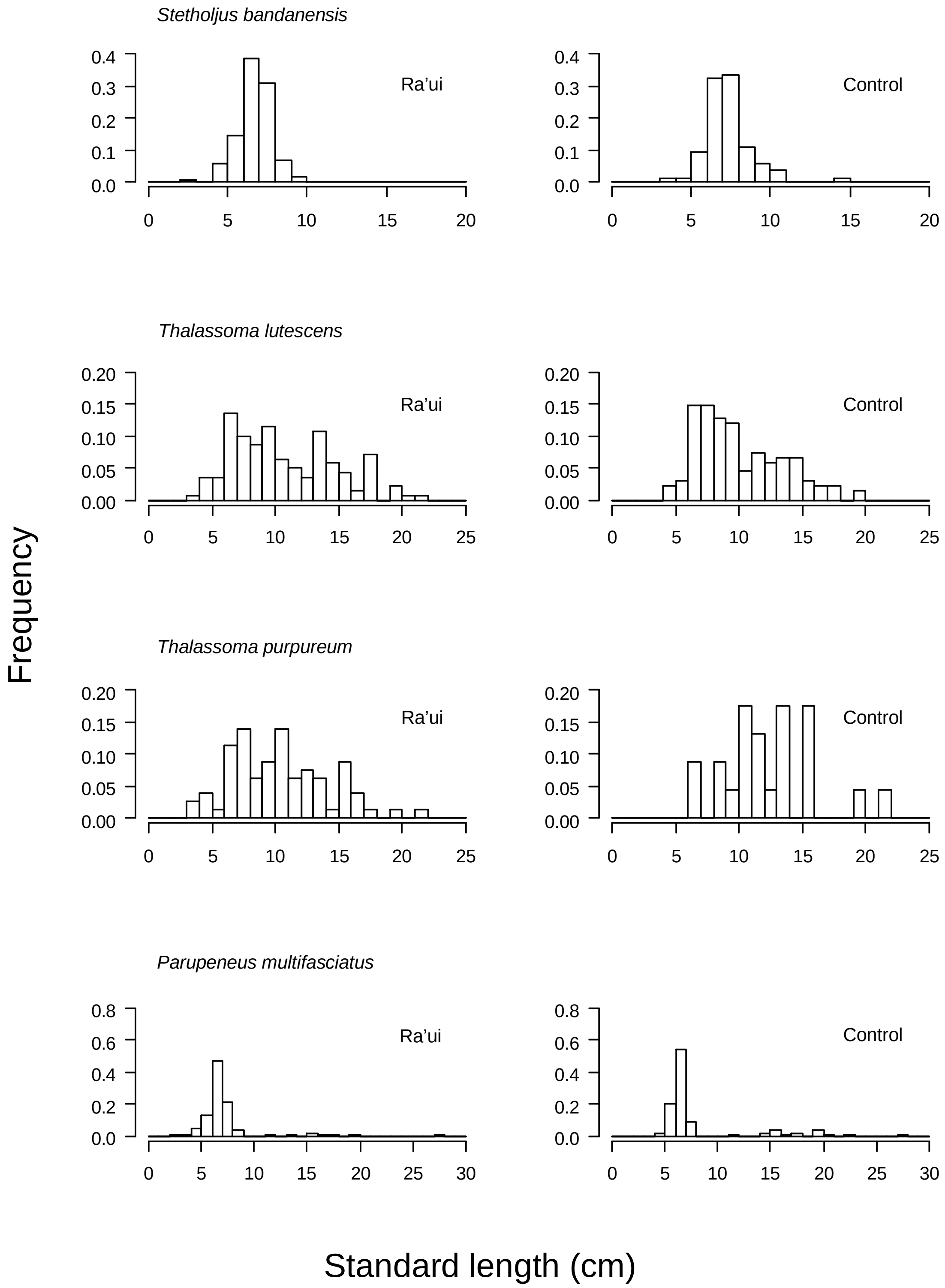


Figure 1 continued. Non-significant length-frequency distributions of each fish species pooled across Ra'ui and Control sites.

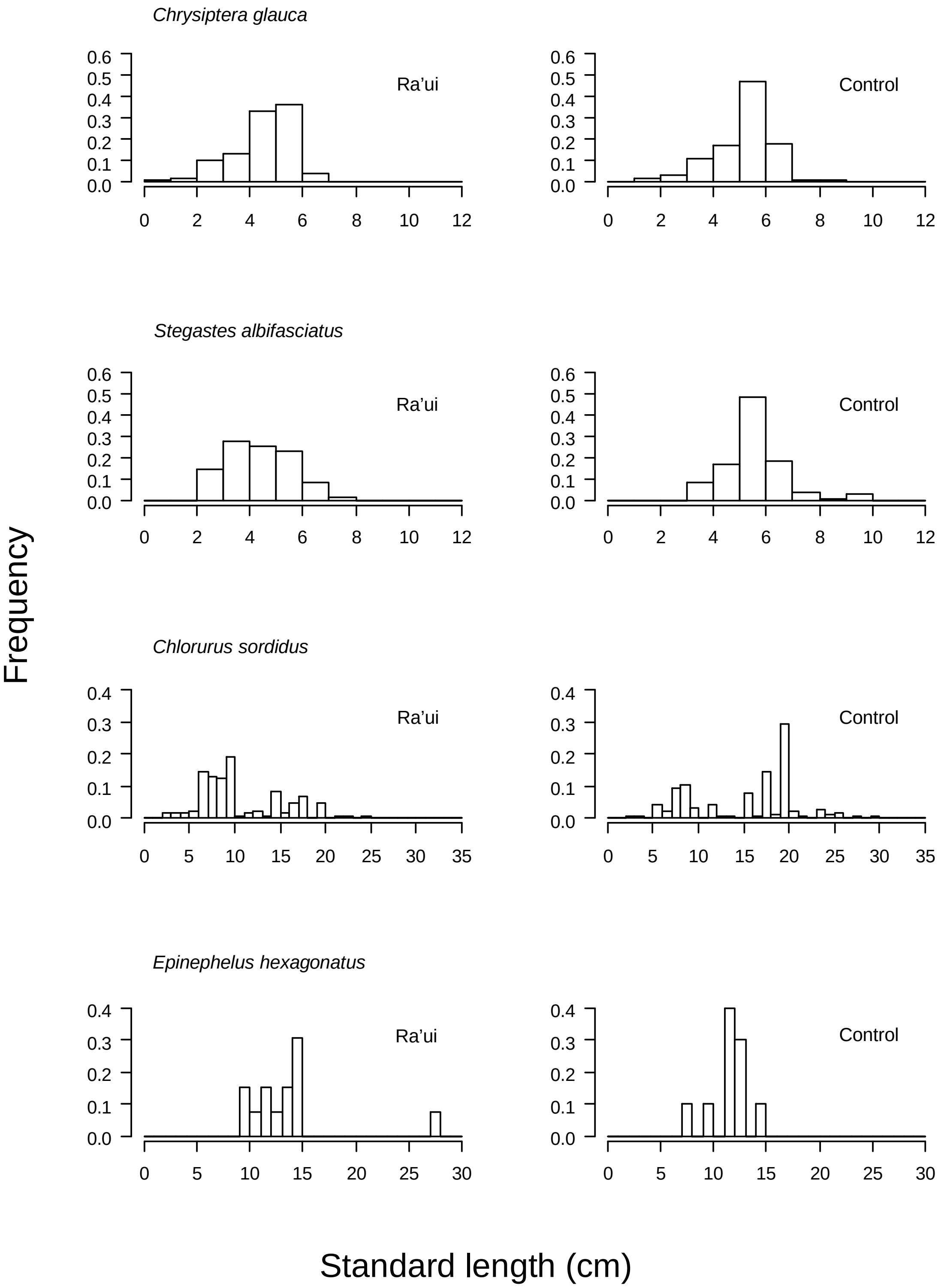


Figure 1 continued. Non-significant length-frequency distributions of each fish species pooled across Ra'ui and Control sites.

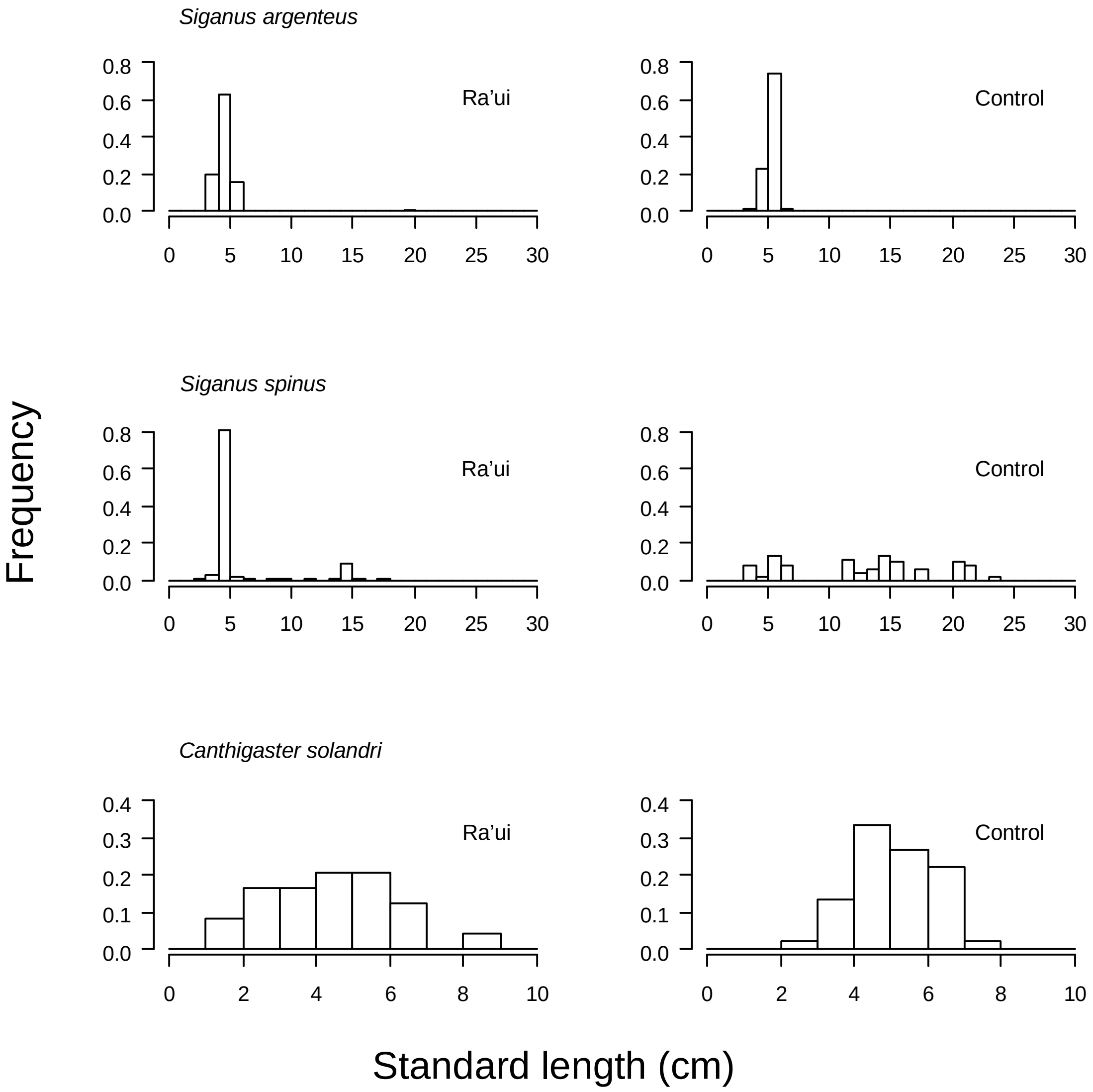


Figure 1 continued. Non-significant length-frequency distributions of each fish species pooled across Ra'ui and Control sites.

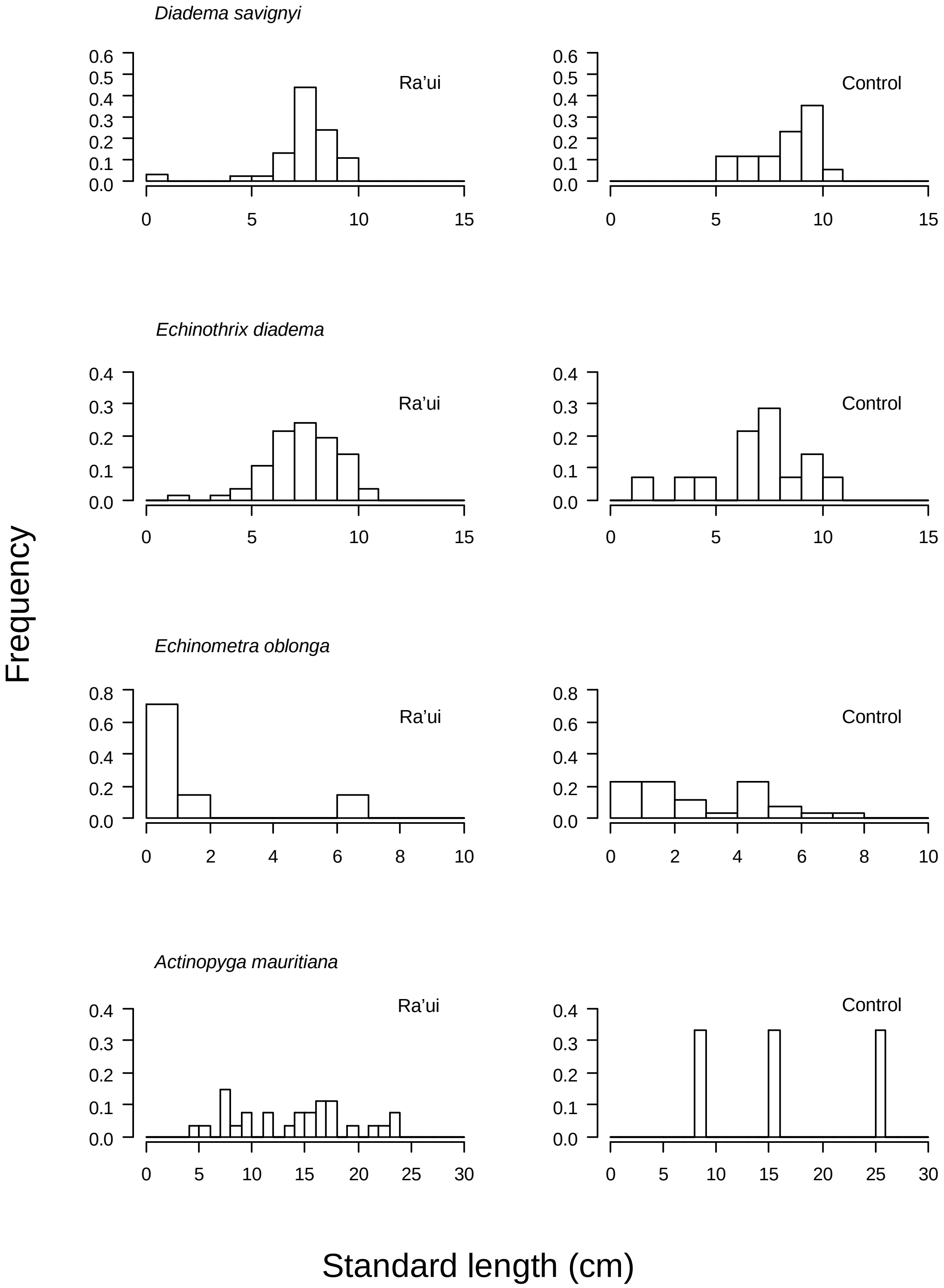


Figure 2. Non-significant length-frequency distributions of each invertebrate species across lagoon Ra'ui and Control sites.

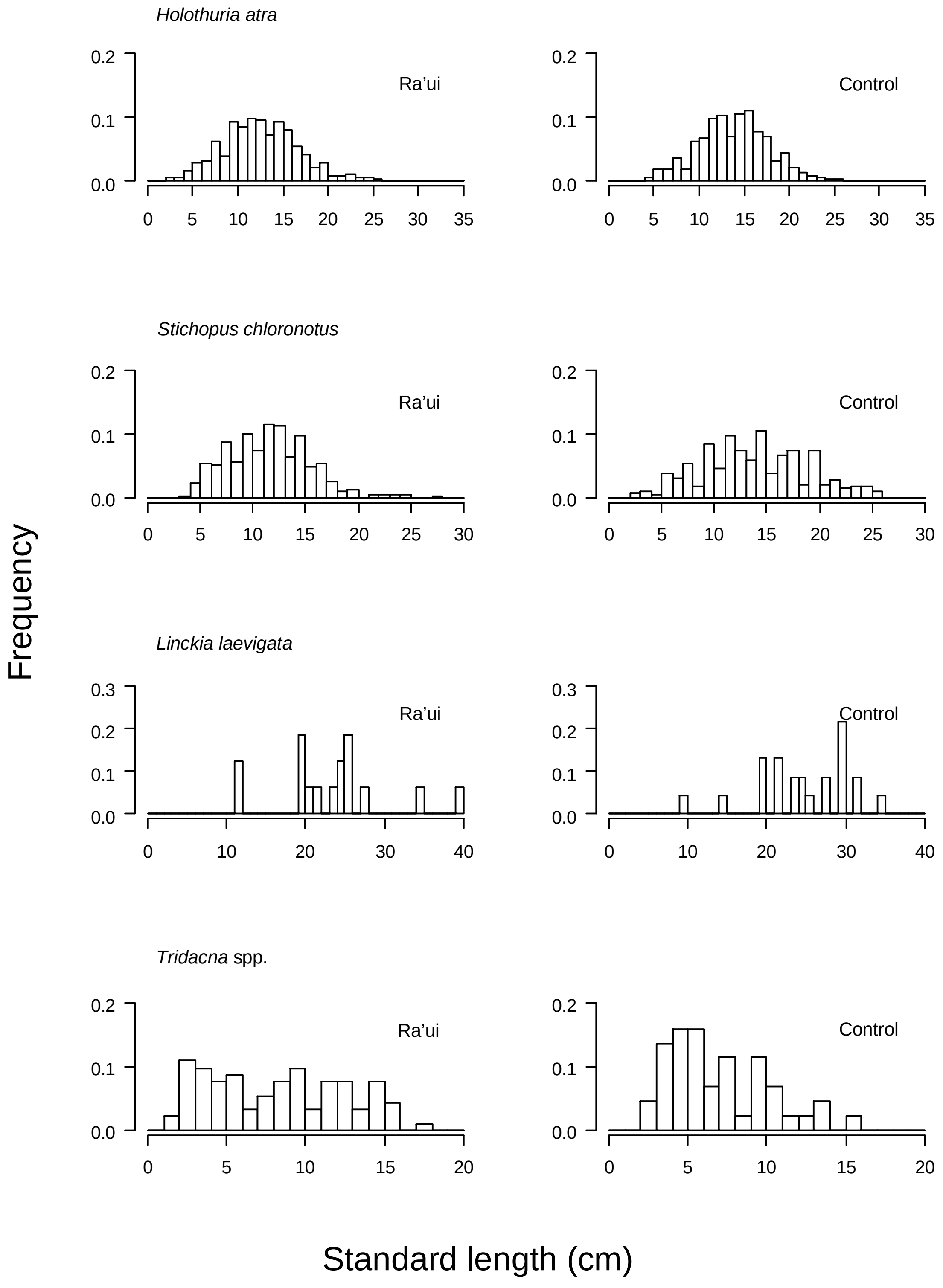


Figure 2 continued. Non-significant length-frequency distributions of each invertebrate species across lagoon Ra'ui and Control sites.

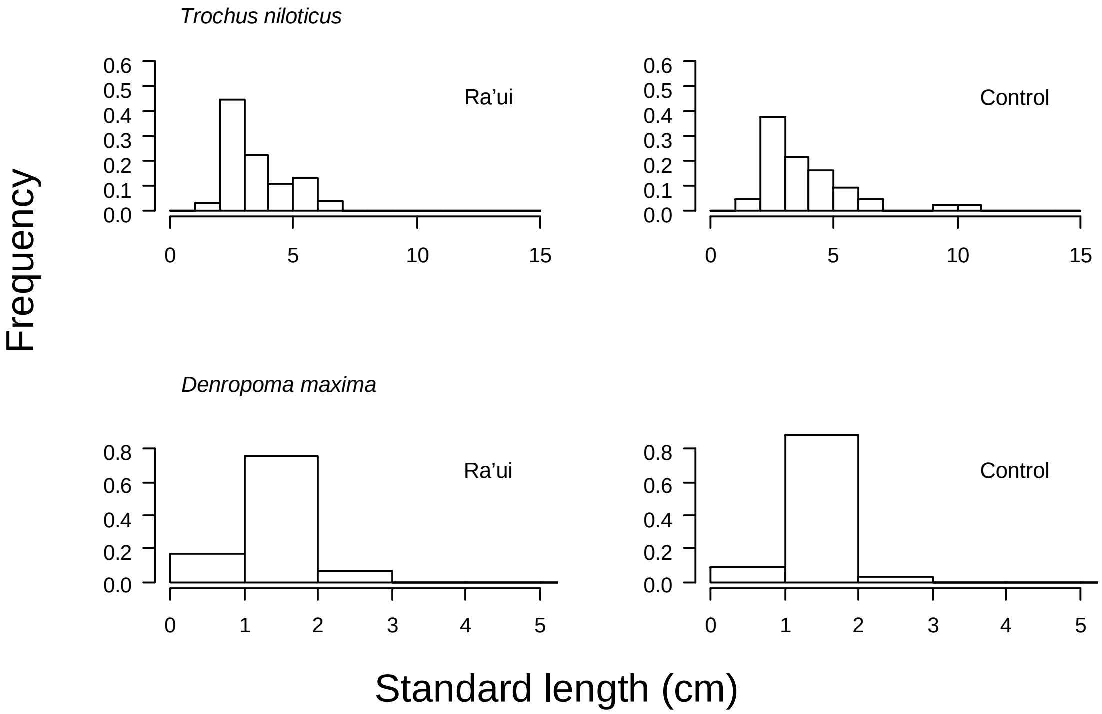


Figure 2 continued. Non-significant length-frequency distributions of each invertebrate species across lagoon Ra’ui and Control sites.

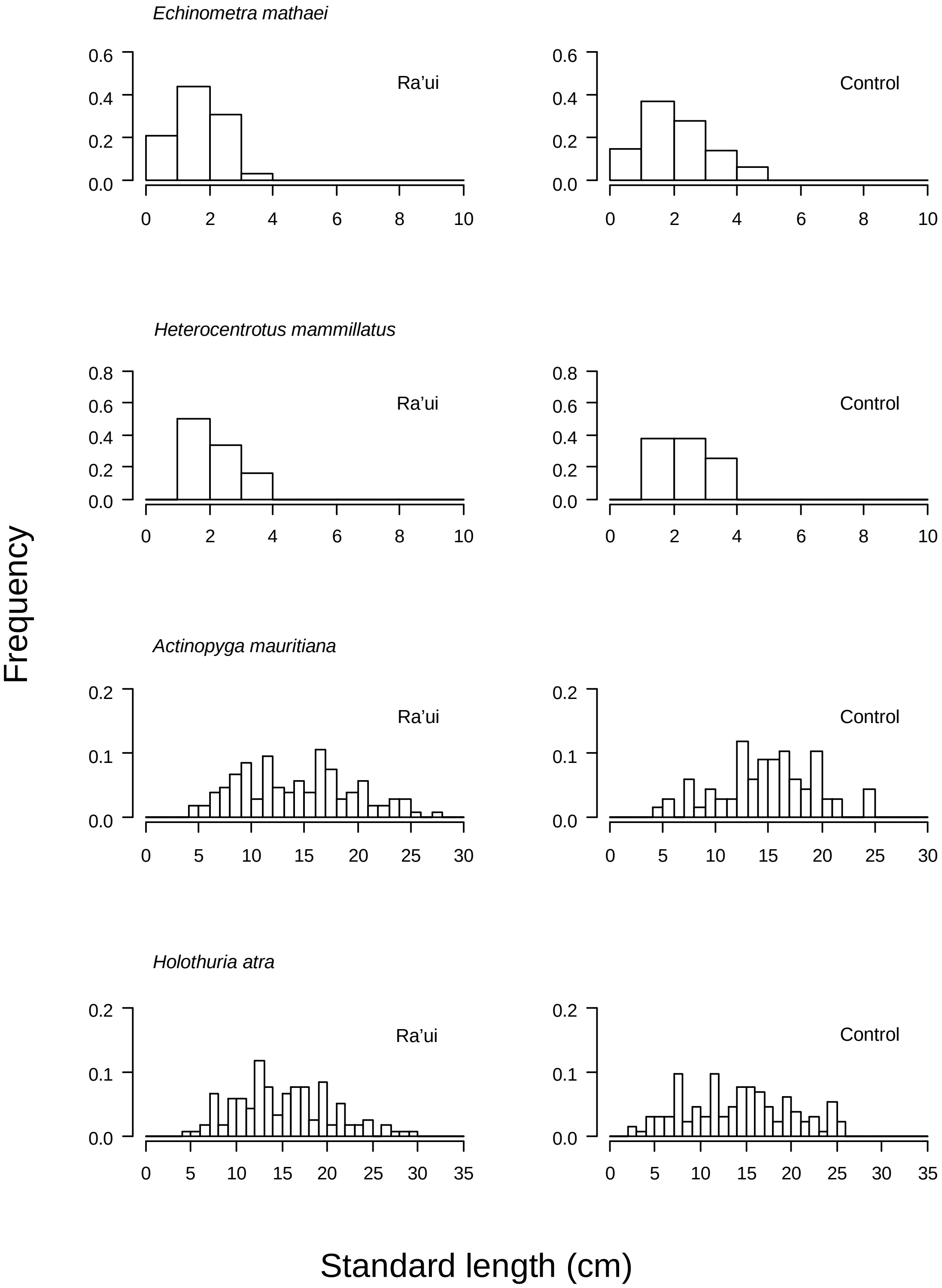


Figure 3. Non-significant length-frequency distributions of each invertebrate species across reef-crest Ra'ui and Control sites.

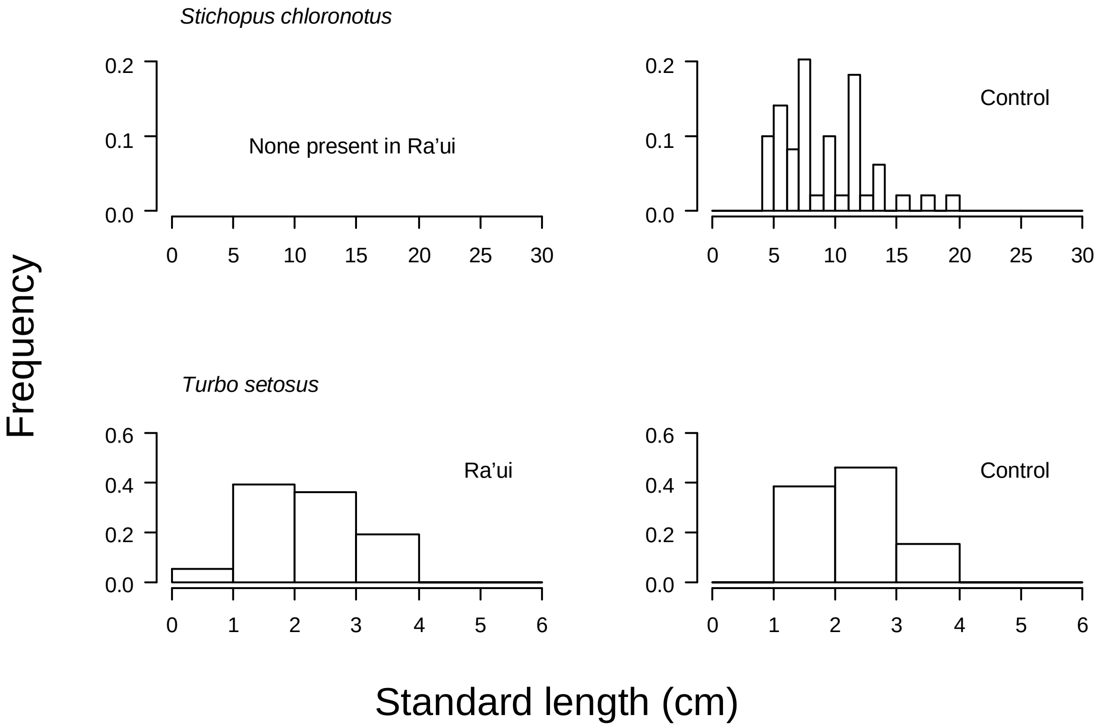


Figure 3 continued. Non-significant length-frequency distributions of each invertebrate species across reef-crest Ra'ui and Control sites.

APPENDIX C

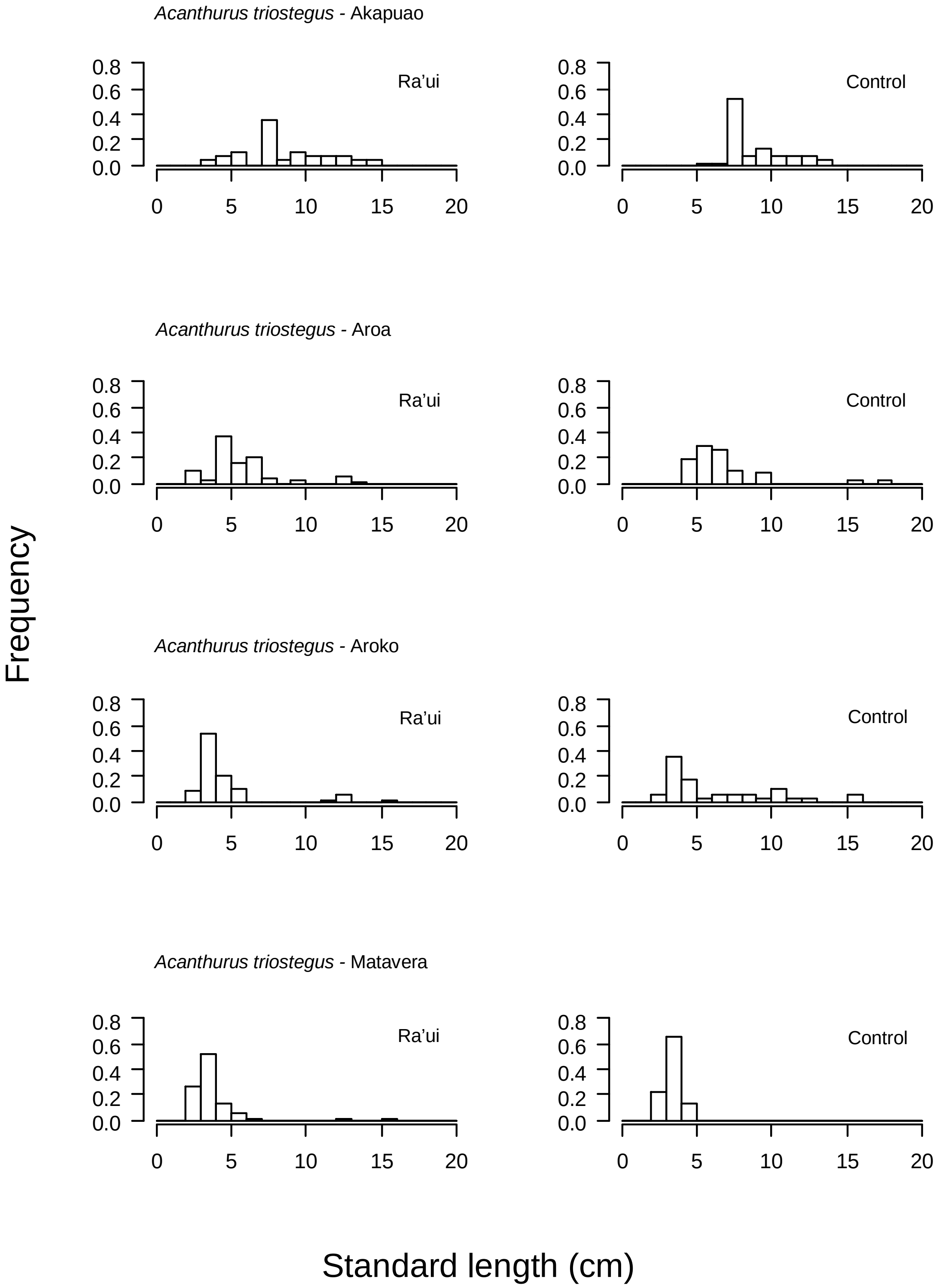


Figure 1. Length-frequency distributions of fish species at Ra'ui and corresponding Control sites.

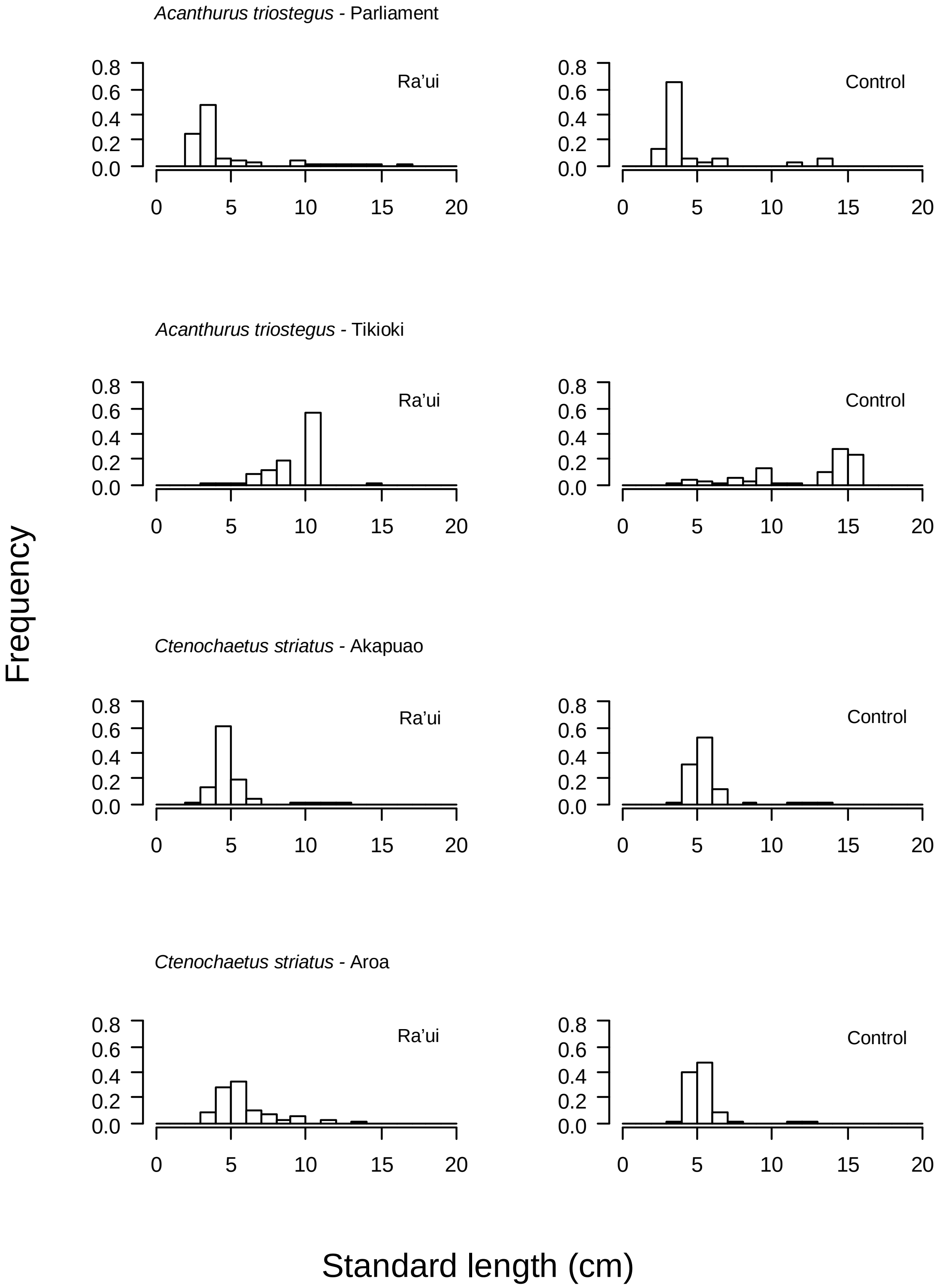


Figure 1 continued. Length-frequency distributions of fish species at Ra’ui and corresponding Control sites.

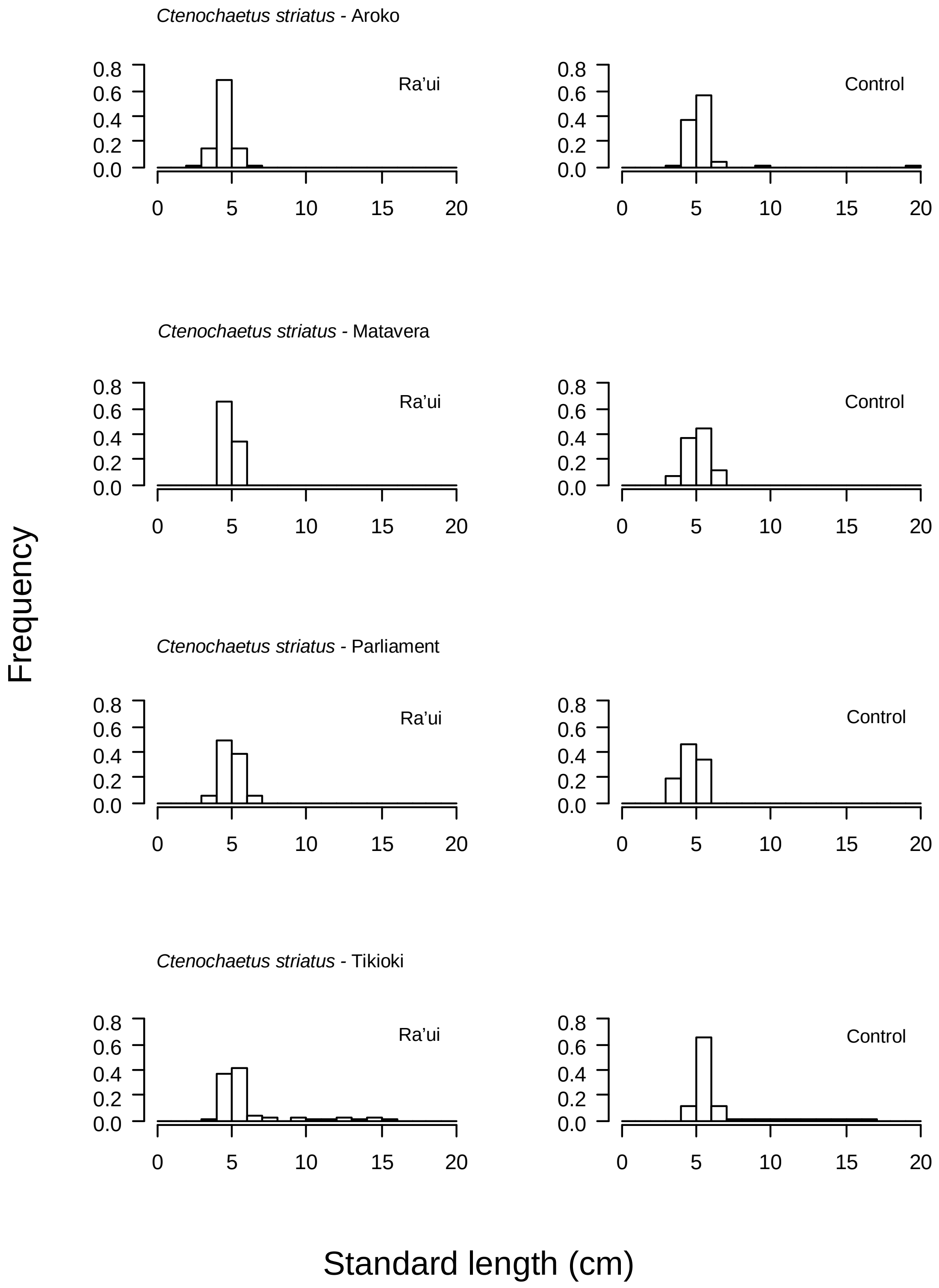
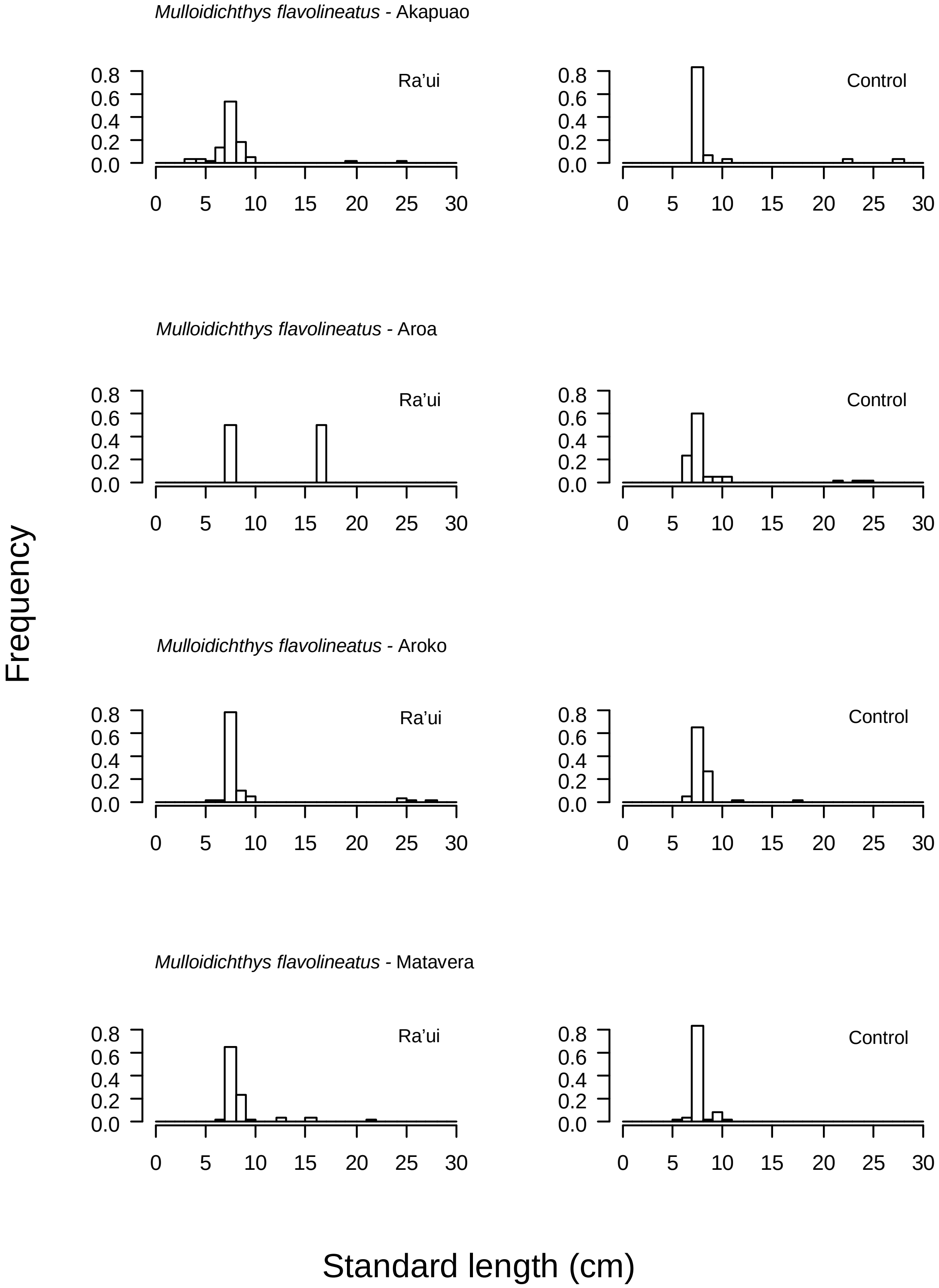


Figure 1 continued. Length-frequency distributions of fish species at Ra'ui and corresponding Control sites.



Mulloidichthys flavolineatus - Akapuao

Mulloidichthys flavolineatus - Aroa

Mulloidichthys flavolineatus - Aroko

Mulloidichthys flavolineatus - Matavera

Figure 1 continued. Length-frequency distributions of fish species at Ra'ui and corresponding Control sites.

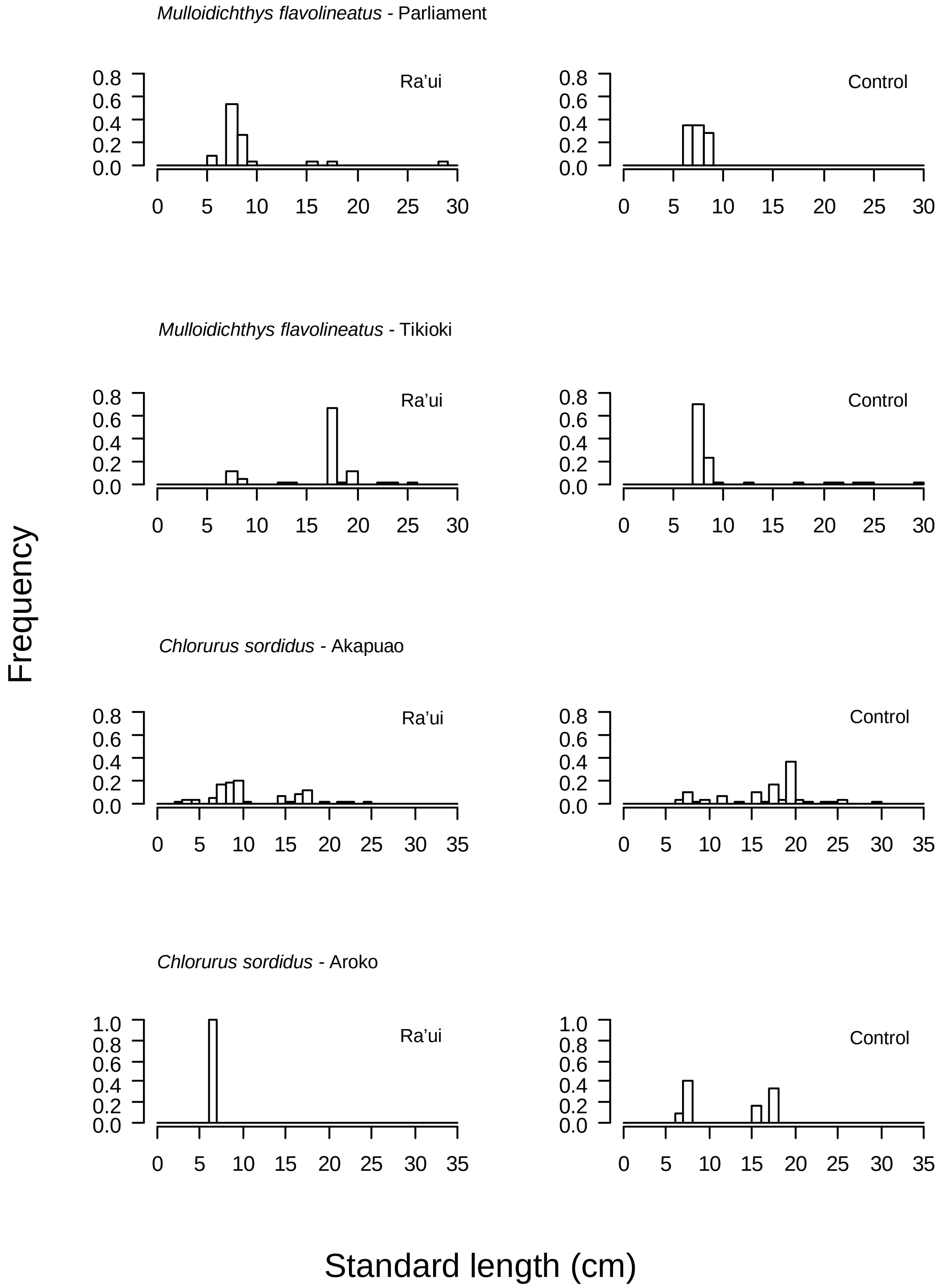


Figure 1 continued. Length-frequency distributions of fish species at Ra'ui and corresponding Control sites.

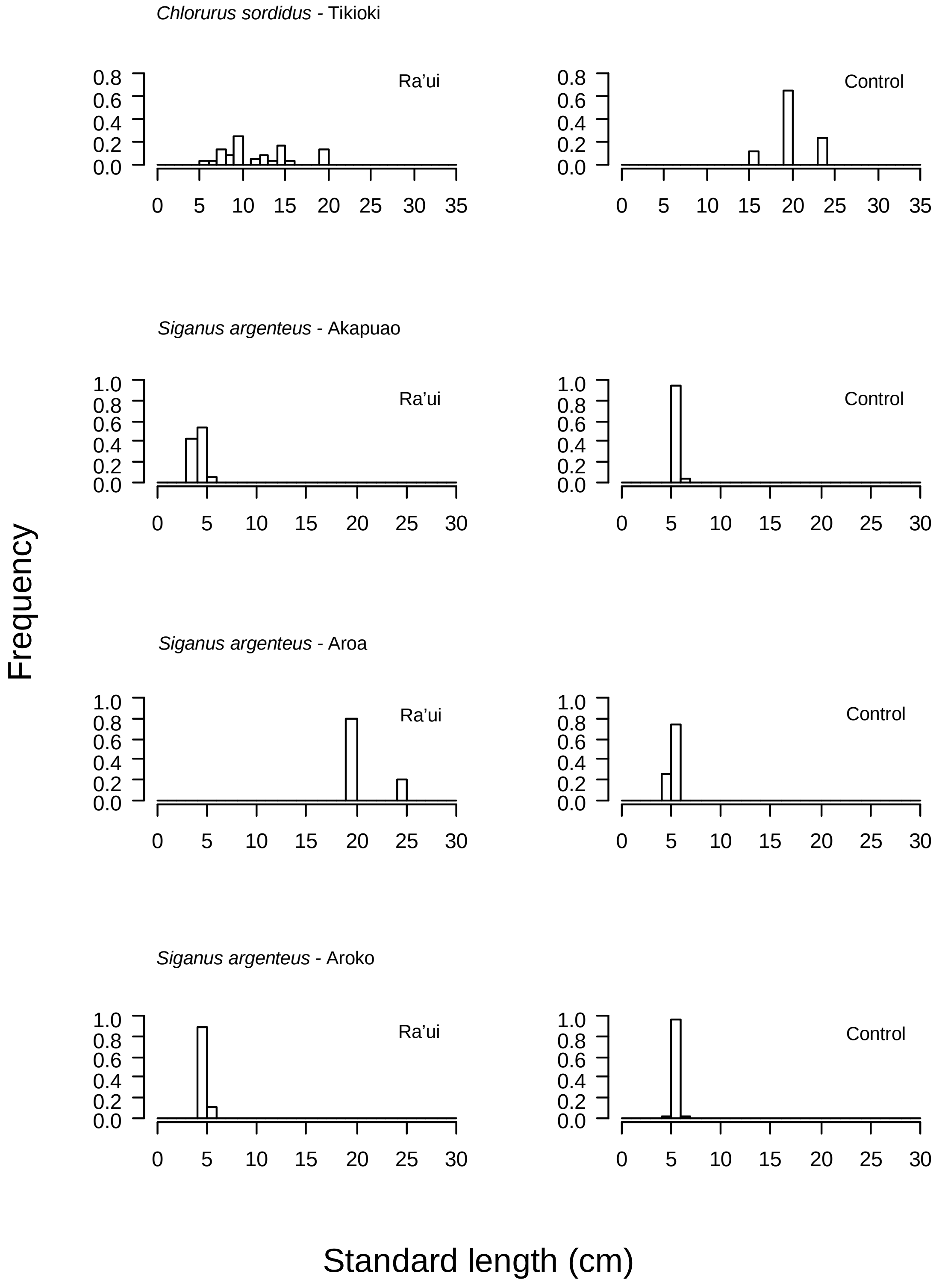
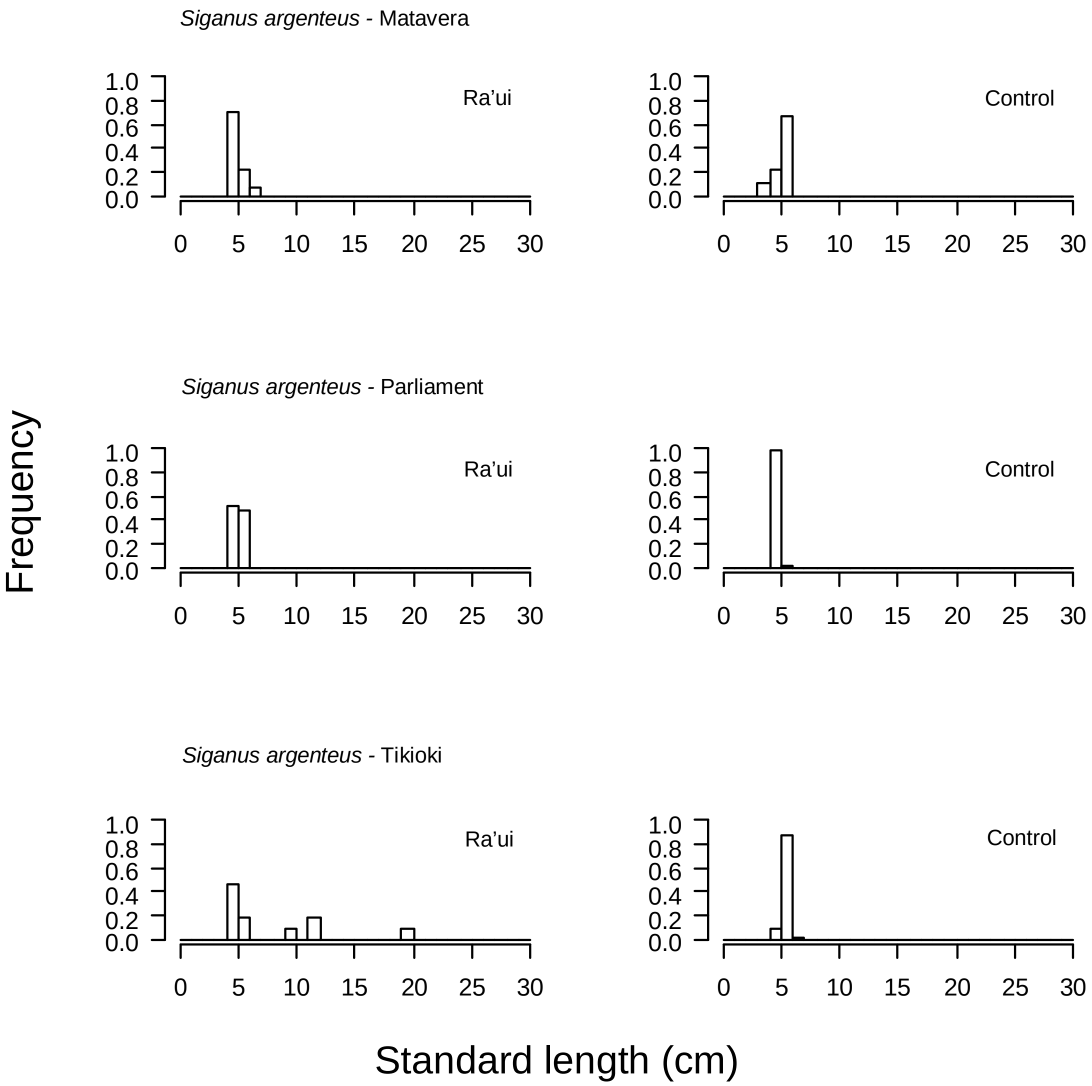


Figure 1 continued. Length-frequency distributions of fish species at Ra'ui and corresponding Control sites.


Siganus argenteus - Matavera

Siganus argenteus - Parliament

Siganus argenteus - Tikioki

Figure 1 continued. Length-frequency distributions of fish species at Ra'ui and corresponding Control sites.

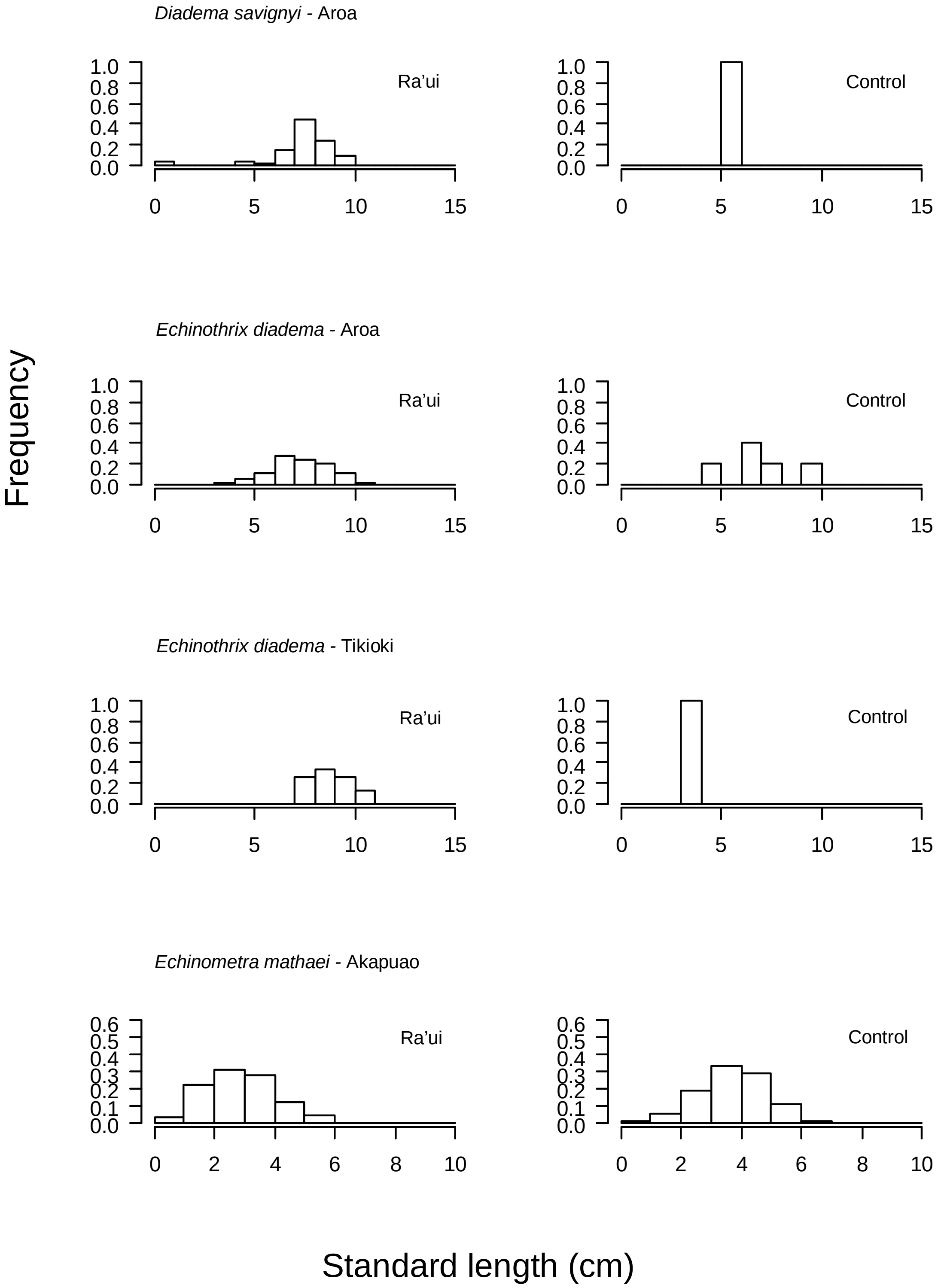


Figure 2. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

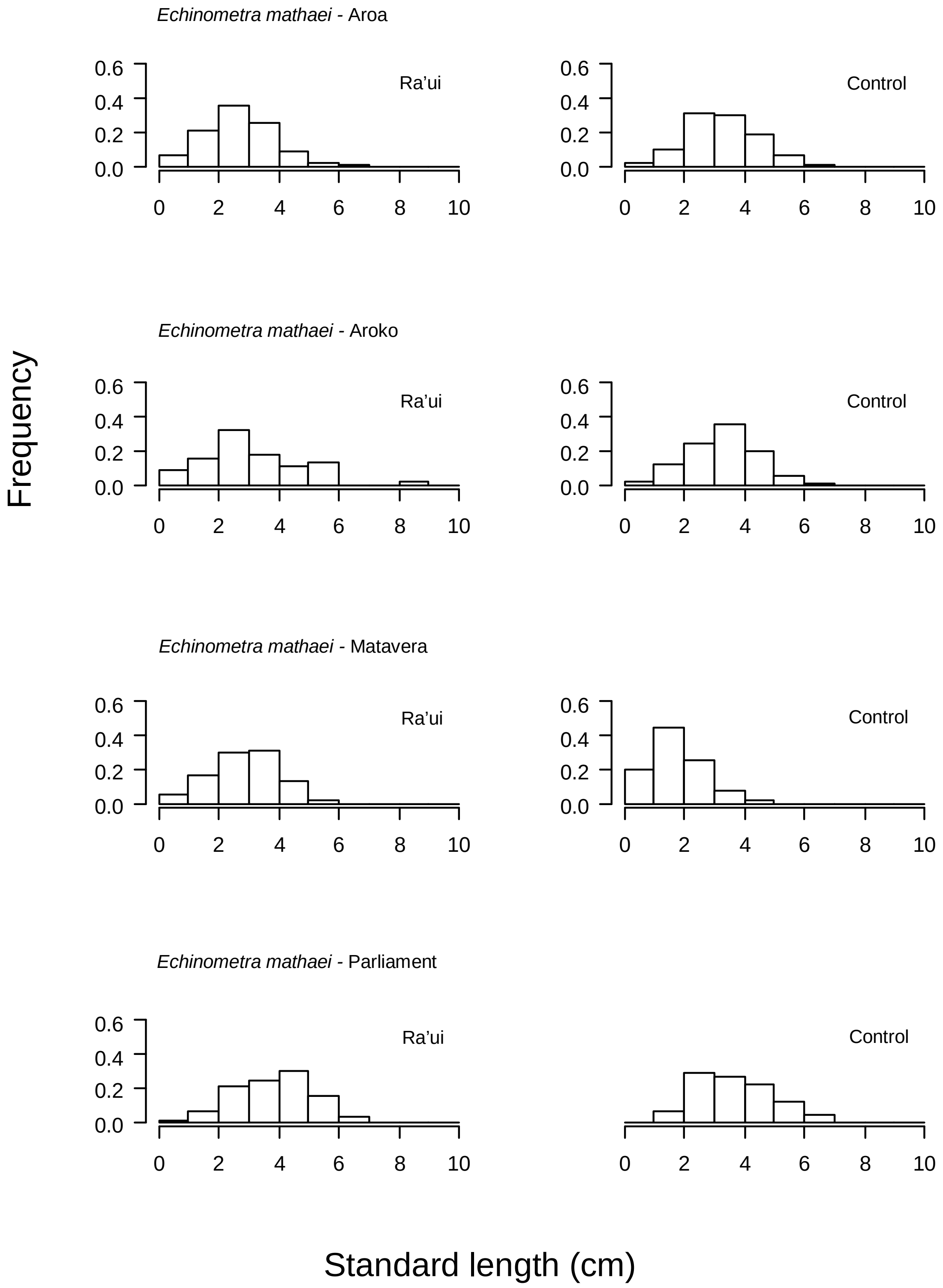


Figure 2 continued. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

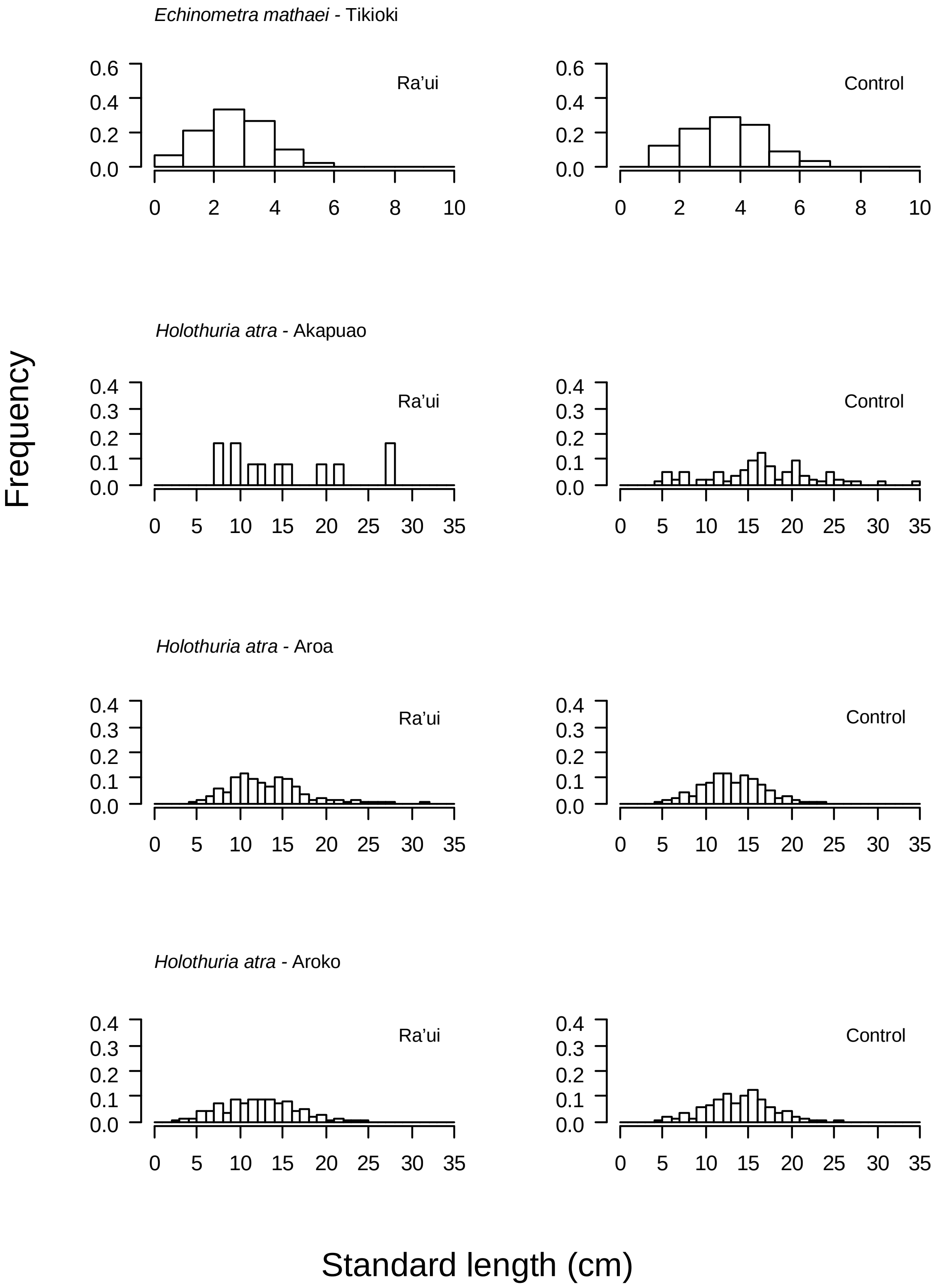


Figure 2 continued. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

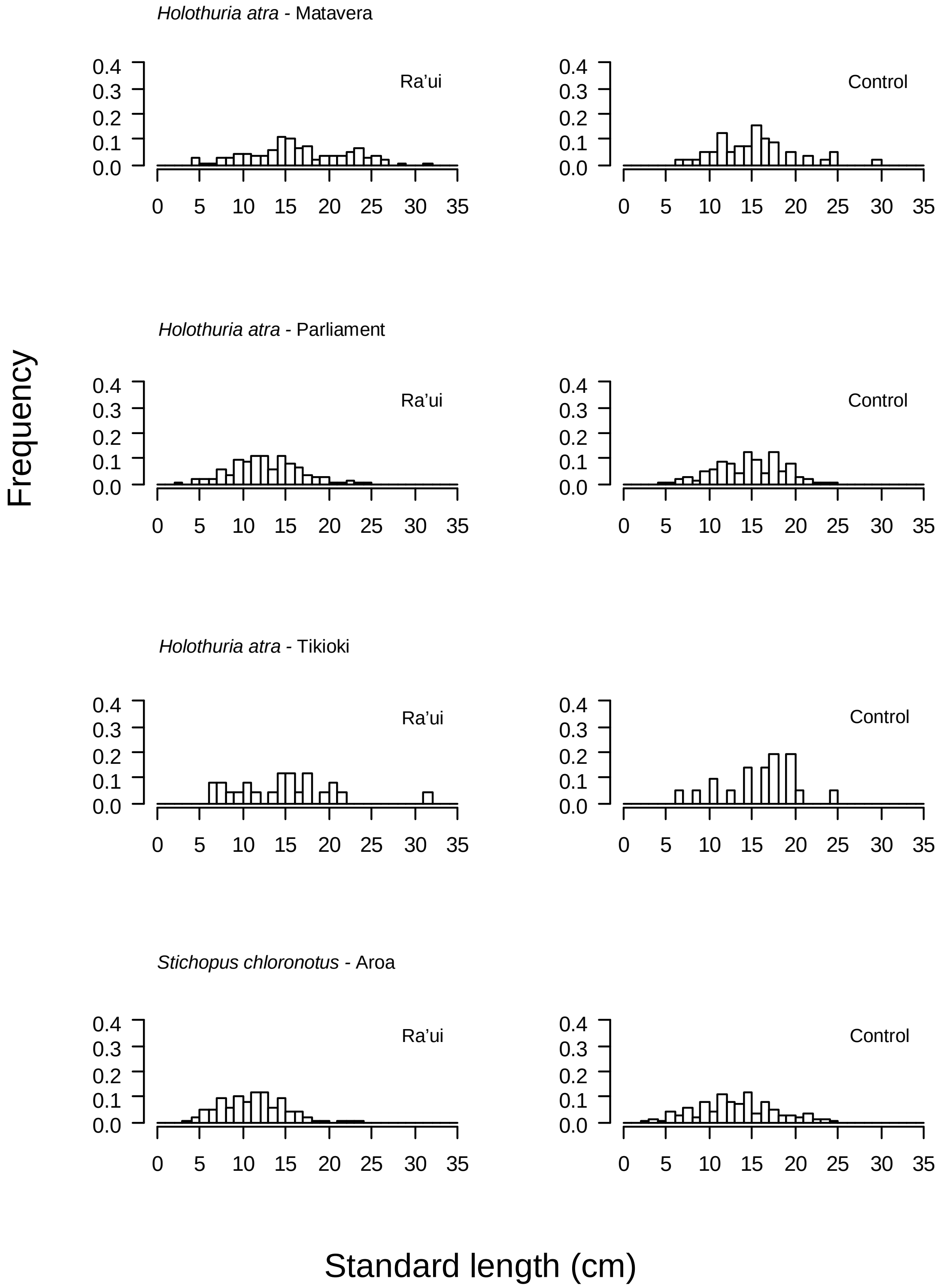


Figure 2 continued. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

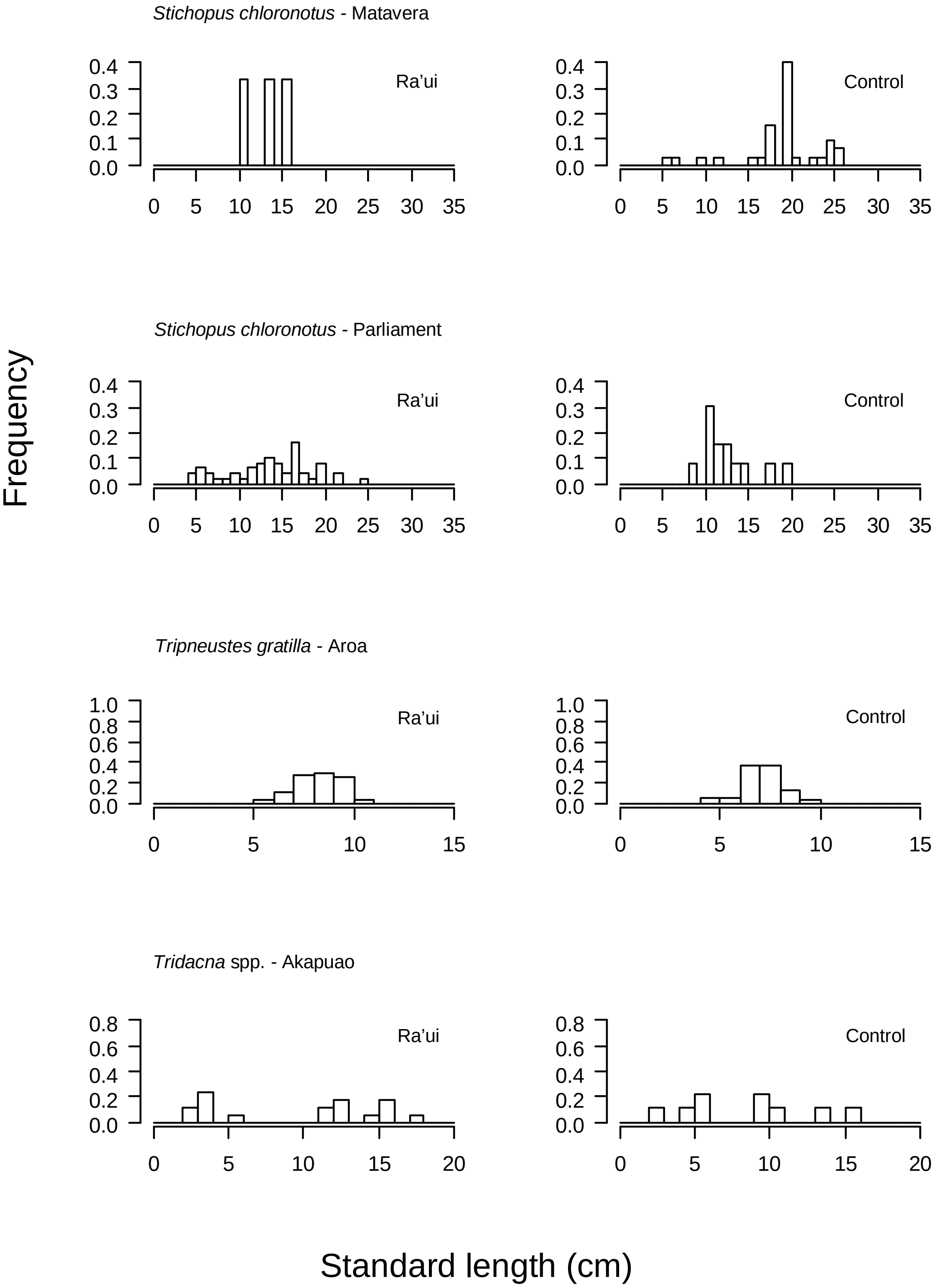


Figure 2 continued. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

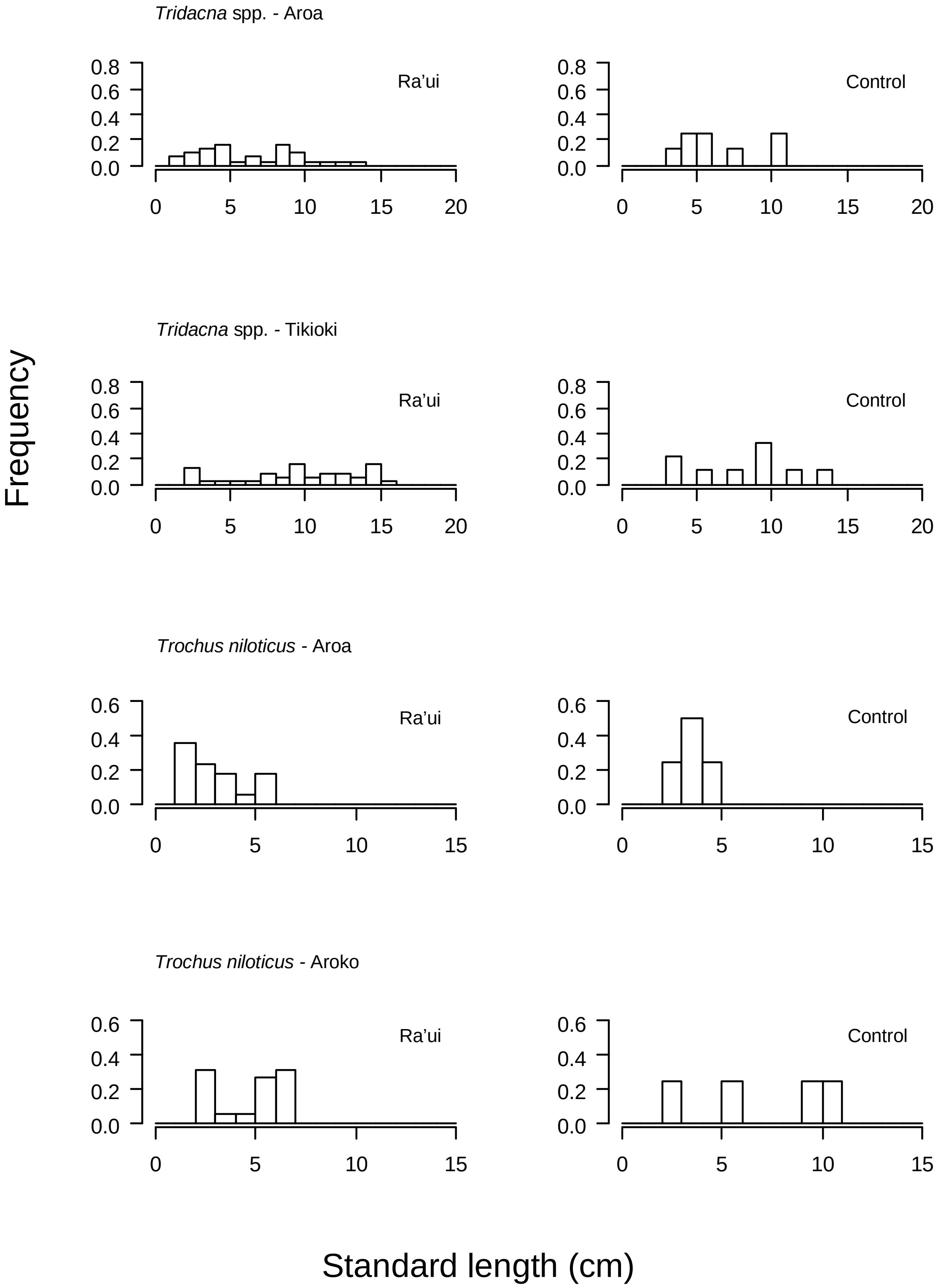


Figure 2 continued. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

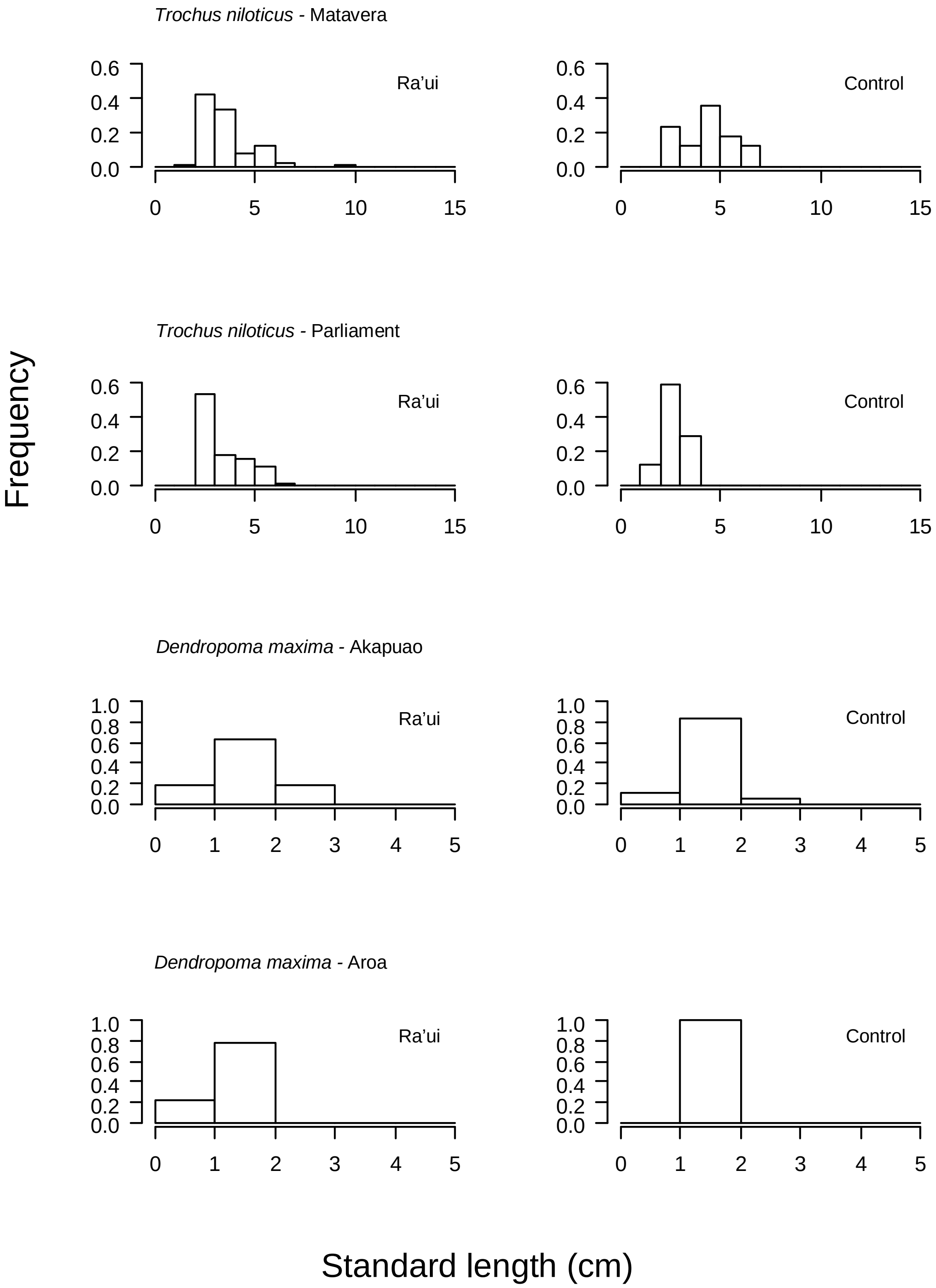


Figure 2 continued. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

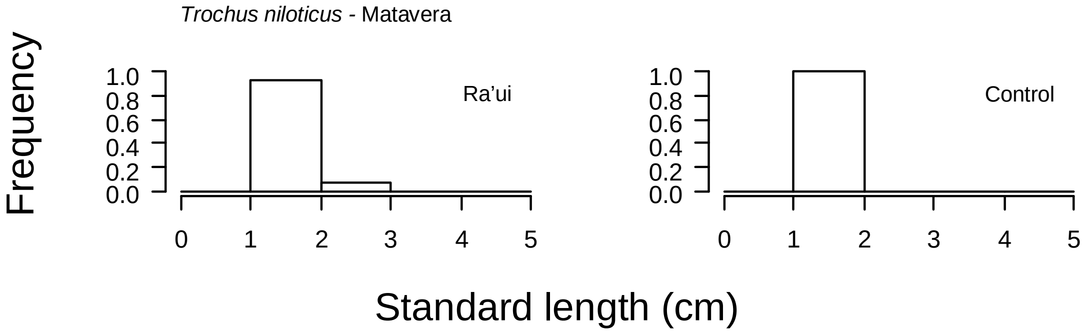


Figure 2 continued. Length-frequency distributions of lagoon invertebrate species at Ra'ui and corresponding Control sites.

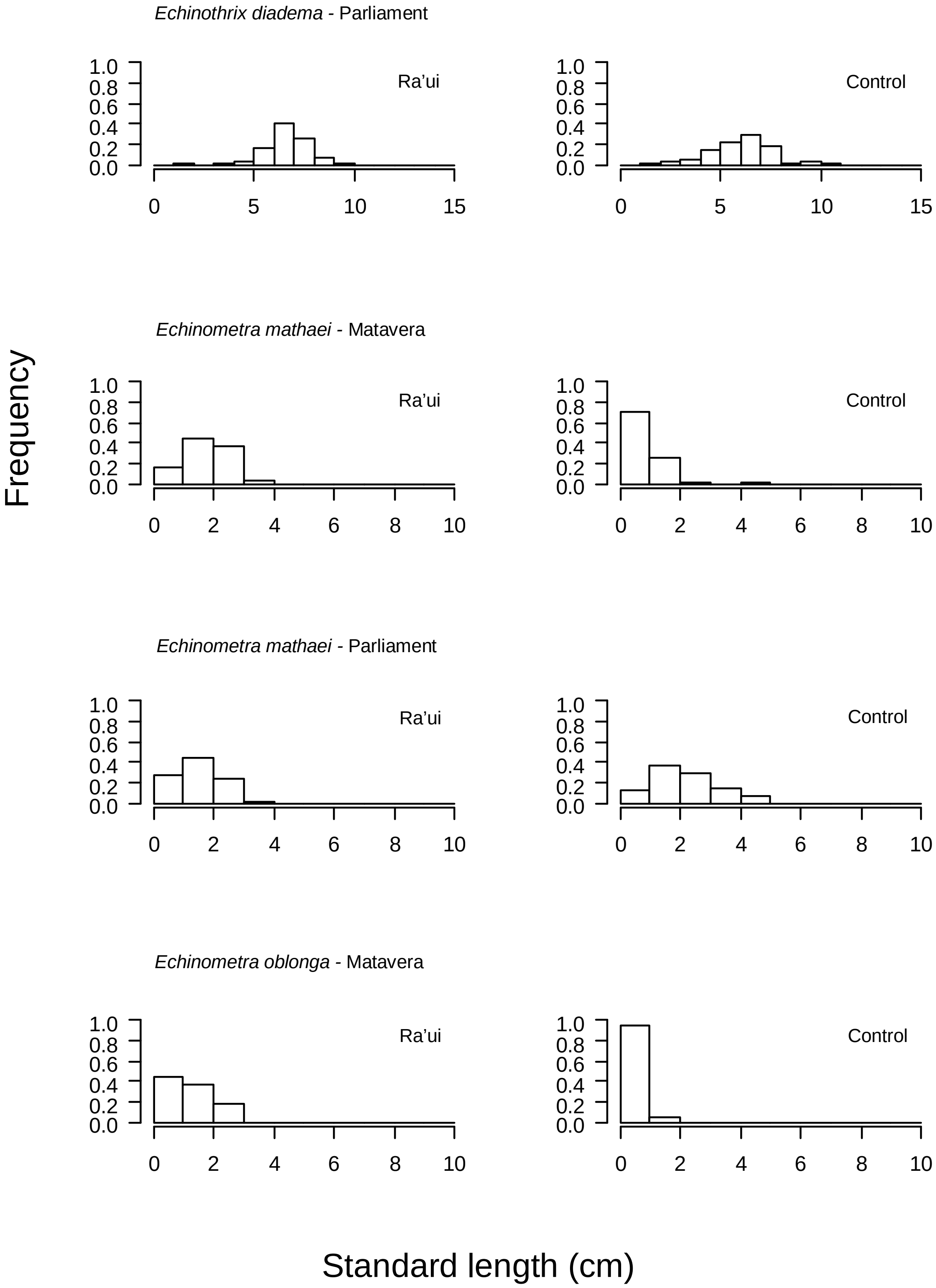


Figure 3. Length-frequency distributions of reef-crest invertebrate species at Ra'ui and corresponding Control sites.

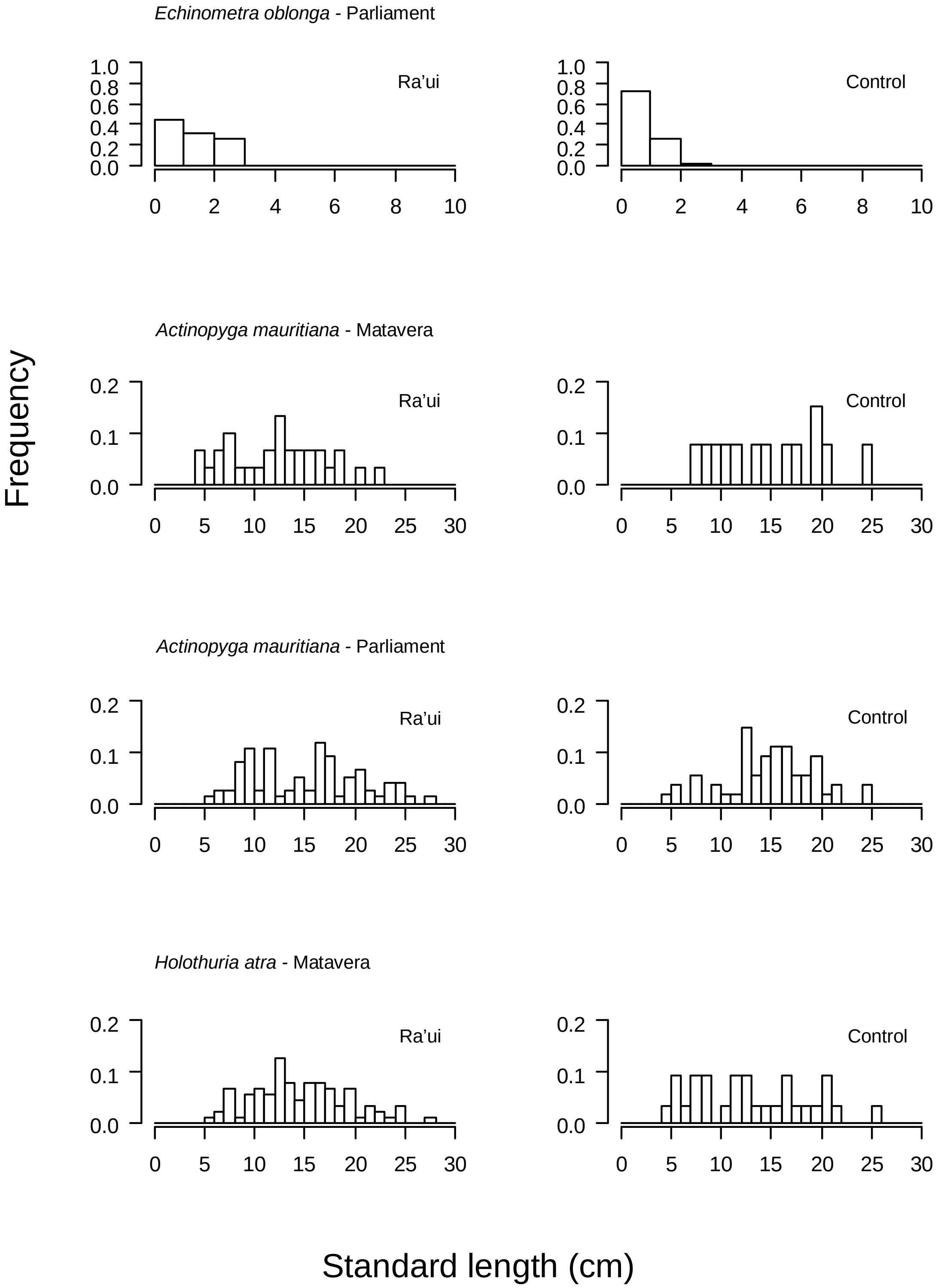


Figure 3 continued. Length-frequency distributions of reef-crest invertebrate species at Ra'ui and corresponding Control sites.

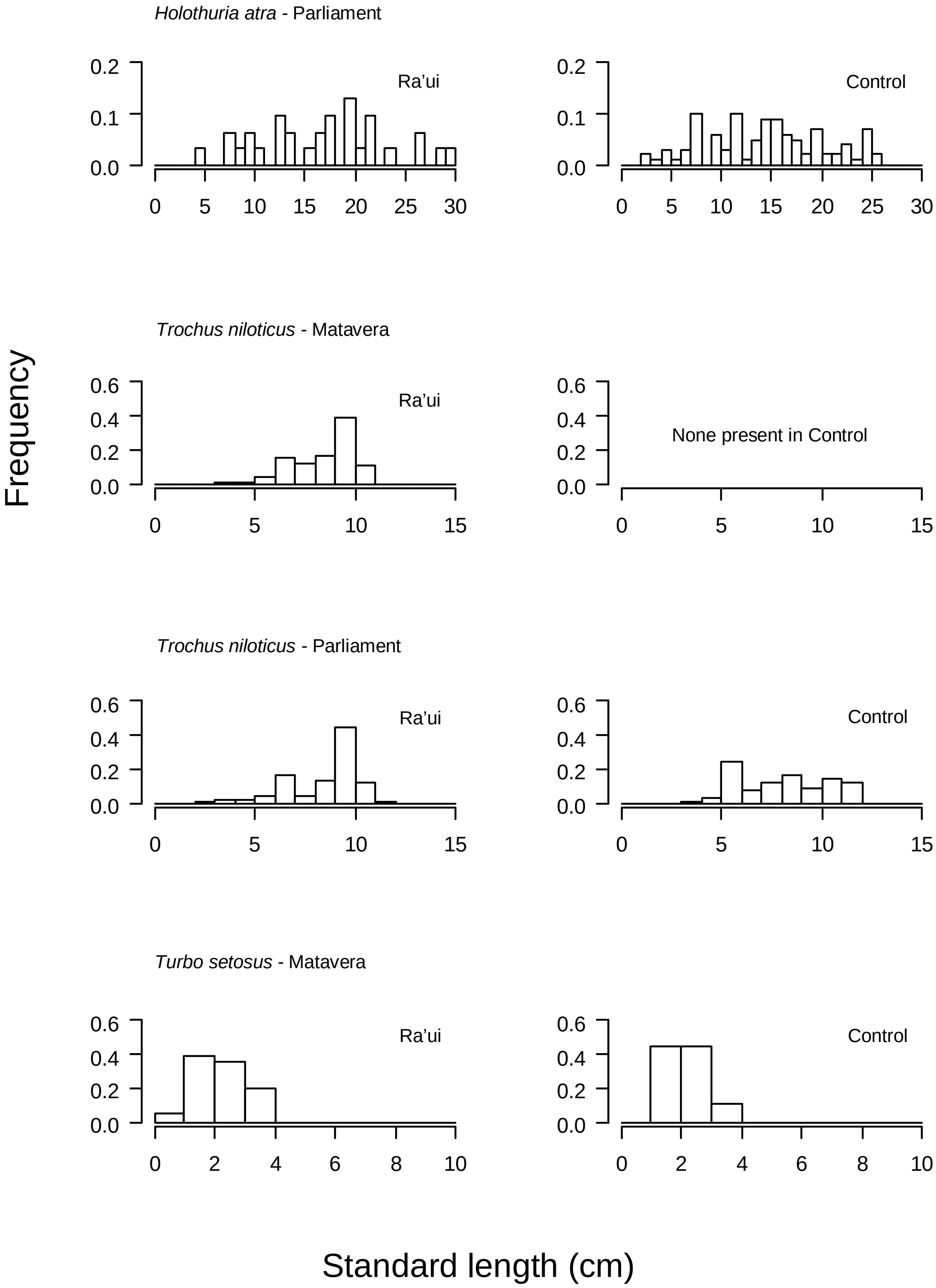


Figure 3 continued. Length-frequency distributions of reef-crest invertebrate species at Ra'ui and corresponding Control sites.

Table 1. Partial correlation coefficients computed in SPSS (SPSS Inc. 2008) while controlling for the effects of the dependent variables of Ra'ui effectiveness A. density; B. mean size; C. maximum size, to assess if there were any correlations between the predictor variables to be included in multiple regressions (Area = Ra'ui area, Crest = distance to reef crest, Pop = human population, and Fish = total fish density).

Control variables	Predictor variables		AREA	CREST	POP	FISH
A: DENSITY	AREA	Correlation	1.000	.633	.400	.431
		p-value (2-tailed)	.	.251	.505	.468
		df	0	3	3	3
	CREST	Correlation	.633	1.000	.298	.646
		p-value (2-tailed)	.251	.	.626	.239
		df	3	0	3	3
	POP	Correlation	.400	.298	1.000	.800
		p-value(2-tailed)	.505	.626	.	.104
		df	3	3	0	3
	FISH	Correlation	.431	.646	.800	1.000
		p-value (2-tailed)	.468	.239	.104	.
		df	3	3	3	0
B: MEAN SIZE	AREA	Correlation	1.000	.047	-.510	-.630
		p-value (2-tailed)	.	.941	.380	.255
		df	0	3	3	3
	CREST	Correlation	.047	1.000	-.334	.112
		p-value (2-tailed)	.941	.	.583	.858
		df	3	0	3	3
	POP	Correlation	-.510	-.334	1.000	.419
		p-value(2-tailed)	.380	.583	.	.483
		df	3	3	0	3
	FISH	Correlation	-.630	.112	.419	1.000
		p-value (2-tailed)	.255	.858	.483	.
		df	3	3	3	0
C: MAXIMUM SIZE	AREA	Correlation	1.000	.548	-.036	-.112
		p-value (2-tailed)	.	.339	.954	.858
		df	0	3	3	3
	CREST	Correlation	.548	1.000	.252	.549
		p-value (2-tailed)	.339	.	.682	.337
		df	3	0	3	3
	POP	Correlation	-.036	.252	1.000	.634
		p-value(2-tailed)	.954	.682	.	.250
		df	3	3	0	3
	FISH	Correlation	-.112	.549	.634	1.000
		p-value (2-tailed)	.858	.337	.250	.
		df	3	3	3	0

Table 2. Multiple regression model summary output from the R statistical platform (R Development Core Team 2006) of Ra'ui characteristics (Ra'ui area, distance to reef crest, human population, and total fish density) as predictors of Ra'ui effectiveness (i.e., the proportion of fish and invertebrates exhibiting greater densities in Ra'ui than corresponding Control sites).

Model Summary					
Residuals:					
1	**2**	**3**	**4**	**5**	**6**
-0.03448	-0.03497	0.06772	-0.04361	0.15590	-0.11055
Coefficients:		**Estimate**	**Standard Error**	**t value**	**Pr (>\\|t|)**
Intercept		0.5618060	0.3675436	1.529	0.266
Distance to reef crest		-0.0004406	0.0003978	-1.107	0.383
Human population		-0.0003868	0.0003557	-1.087	0.390
Total fish density		0.2998765	0.2540733	1.180	0.359
Residual standard error:		0.1507 on 2 degrees of freedom			
Multiple R-Squared:		0.5132		**Adjusted R-squared:**	-0.2169
F-statistic:		0.7029 on 3 and 2 DF		**p-value:**	0.6323

Table 3. Multiple regression model summary output from the R statistical platform (R Development Core Team 2006) of Ra'ui characteristics (Ra'ui area, distance to reef crest, human population, and total fish density) as predictors of Ra'ui effectiveness (i.e., the proportion of fish and invertebrates exhibiting greater mean size in Ra'ui than corresponding Control sites).

Model Summary					
Residuals:					
1	**2**	**3**	**4**	**5**	**6**
-0.003510	0.002730	-0.018528	-0.038297	0.105229	-0.042164
	Coefficients:	**Estimate**	**Standard Error**	**t value**	**Pr (>\\|t|)**
	Intercept	0.625645	0.090947	6.879	0.00629
	Ra'ui area	-0.006156	0.002010	-3.063.	0.05488
	Total fish density	-0.199746	0.069720	-2.865	0.06432
Residual standard error:		0.06995 on 3 degrees of freedom			
Multiple R-Squared:		0.9145		**Adjusted R-squared:**	0.8575
F-statistic:		16.05 on 2 and 3 DF		**p-value:**	0.02500

Table 4. Multiple regression model summary output from the R statistical platform (R Development Core Team 2006) of Ra'ui characteristics (Ra'ui area, distance to reef crest, human population, and total fish density) as predictors of Ra'ui effectiveness (i.e., the proportion of fish and invertebrates exhibiting greater maximum size in Ra'ui than corresponding Control sites).

<table>
<tr><th colspan="6">Model Summary</th></tr>
<tr><td colspan="6">Residuals:</td></tr>
<tr><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td></tr>
<tr><td>-0.06936</td><td>-0.04177</td><td>0.03597</td><td>-0.03217</td><td>0.12495</td><td>-0.01762</td></tr>
<tr><td colspan="2">Coefficients:</td><td>Estimate</td><td>Standard Error</td><td>t value</td><td>Pr (>\|t|)</td></tr>
<tr><td colspan="2">Intercept</td><td>0.7400337</td><td>0.1511208</td><td>4.897</td><td>0.0393</td></tr>
<tr><td colspan="2">Ra'ui area</td><td>-0.0078659</td><td>0.0037490</td><td>-2.098</td><td>0.1708</td></tr>
<tr><td colspan="2">Distance to reef crest</td><td>0.0003671</td><td>0.0003408</td><td>1.077</td><td>0.3940</td></tr>
<tr><td colspan="2">Total fish density</td><td>-0.2008077</td><td>0.1315512</td><td>-1.526</td><td>0.2664</td></tr>
<tr><td colspan="2">Residual standard error:</td><td colspan="4">0.1114 on 2 degrees of freedom</td></tr>
<tr><td colspan="2">Multiple R-Squared:</td><td colspan="2">0.8202</td><td>Adjusted R-squared:</td><td>0.5506</td></tr>
<tr><td colspan="2">F-statistic:</td><td colspan="2">3.042 on 3 and 2 DF</td><td>p-value:</td><td>0.2571</td></tr>
</table>

REFERENCES

Adams T. (1998). The interface between traditional and modern methods of fishery management in the Pacific Islands. *Ocean & Coastal Management*, 40(2-3): 127-142.

Agardy T., Bridgewater P., Crosby M., Day J., Dayton P., Kenchington R., Laffoley D., McConney P., Murray P., Parks J. & Peau L. (2003). Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 13(4): 353-367.

Al-Jufaili S., Al-Jabri M., Al-Baluchi A., Baldwin R.M., Wilson S.C., West F. & Matthews A.D. (1999). Human impacts on coral reefs in the Sultanate of Oman. *Estuarine, Coastal and Shelf Science*, 49: 65-74.

Ama A. (2003). Maeva. Rites of passage: the highlights of family life. In: Akono'anga Maori; Cook Islands Culture. (ed. Crocombe RM). pp. 119-125. Institute of Pacific Studies, University of the South Pacific.

Anderson M., J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26: 32-46.

Andrefouet S., Pages J. & Tartinville B. (2001). Water renewal time for classification of atoll lagoons in the Tuamotu Archipelago (French Polynesia). *Coral Reefs*, 20(4): 399-408.

Ashworth J.S., Ormond R.F.G. & Sturrock H.T. (2004). Effects of reef-top gathering and fishing on invertebrate abundance across take and no-take zones. *Journal of Experimental Marine Biology and Ecology*, 303(2): 221-242.

Aswani S., Albert S., Sabetian A. & Furusawa T. (2007). Customary management as precautionary and adaptive principles for protecting coral reefs in Oceania. *Coral Reefs*, 26(4): 1009-1021.

Aswani S. & Weiant P. (2004). Scientific evaluation in women's participatory management: Monitoring marine invertebrate refugia in the Solomon Islands. *Human Organization*, 63(3): 301-319.

Bakus G.J. (1973). The biology and ecology of tropical holothurians. In: Biology and geology of coral reefs (eds. Jones OA & Endean R). pp. 325-367. Academic Press, New York.

Balmford A., Gravestock P., Hockley N., McClean C.J. & Roberts C.M. (2004). The worldwide costs of marine protected areas. *Proceedings of the National Academy of Sciences of the United States of America*, 101(26): 9694-9697.

Barclay R.F.R. (2001). Kaitiakitanga, raahui and ra'ui: traditional resource management ethics in Aotearoa and the Cook Islands. *Te Taarere aa Tawhaki; Journal of the Waikato University College*: 106-117.

Begg G.A., Mapstone B.D., Williams A.J., Adams S., Davies C.R. & Lou D.C. (2005). Multivariate life-history indices of exploited coral reef fish populations used to measure the performance of no-take zones in a marine protected area. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(3): 679-692.

Bellwood D.R., Hughes T.P., Folke C. & Nystrom M. (2004). Confronting the coral reef crisis. *Nature*, 429(24 June): 827-833.

Blueweiss L., Fox H., Kudzman D., Peters R. & Sams S. (1978). Relationships between body size and some life history parameters. *Oecologia*, 37(257-272).

Blyth-Skyrme R.E., Kaiser M.J., Hiddink J.G., Edwards-Jones G. & Hart P.J.B. (2006). Conservation benefits of temperate marine protected areas: variation among fish species. *Conservation Biology*, 20(3): 811-820.

Boersma P.D. & Parrish J.K. (1999). Limiting abuse: marine protected areas, a limited solution. *Ecological Economics*, 31(2): 287-304.

Bohnsack J.A. (1998). Application of marine reserves to reef fisheries management. *Austral Ecology*, 23(3): 298-304.

Botsford L.W. (2005). Potential contributions of marine reserves to sustainable fisheries: Recent modelling results. *Bulletin of Marine Science*, 76(2): 245-259.

Botsford L.W., Castilla J.C. & Peterson C.H. (1997). The Management of Fisheries and Marine Ecosystems. *Science*, 277(5325): 509-515.

Botsford L.W., Hastings A. & Gaines S.D. (2001). Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters*, 4(2): 144-150.

Botsford L.W., Micheli F. & Hastings A. (2003). Principles for the design of marine reserves. *Ecological Applications*, 13(1 Supplement): S25-S31.

Bour W. (1990). The Fishery Resources of Pacific Island Countries. Part Three: Trochus. *FAO fisheries technical paper*. Food and agriculture organisation of the United Nations. Noumea, New Caledonia. 89 pp.

Box G.E.P. & Tiao G.C. (1975). Intervention Analysis with Applications to Economic and Environmental Problems. *Journal of the American Statistical Association*, 70(349): 70-79.

Buechner M. (1987). Conservation in insular parks: Simulation models of factors affecting the movement of animals across park boundaries. *Biological Conservation*, 41(1): 57-76.

Buse J. & Taringa R. (1996). Cook Islands Maori dictionary. Research School of Pacific and Asian Studies, Australian National University, Canberra. 712 pp.

Buxton C.D. & Smale M.J. (1989). Abundance and Distribution Patterns of Three Temperate Marine Reef Fish (Teleostei: Sparidae) in Exploited and Unexploited Areas Off the Southern Cape Coast. *Journal of Applied Ecology*, 26(2): 441-451.

Byers J.E. & Noonburg E.G. (2007). Poaching, enforcement, and the efficacy of marine reserves. *Ecological Applications*, 17: 1851-1856.

Calamia M. (1999). A methodology for incorporating traditional ecological knowledge with geographic information systems for marine resource management in the Pacific. *SPC Traditional Marine Resource Management and Knowledge Information Bulletin*. 10. 2-12 pp.

Chapman M.R. & Kramer D.L. (1999). Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: Effects of reserve protection and habitat characteristics. *Marine Ecology Progress Series*, 181: 81-96.

Chateau O. & Wantiez L. (2005). Comparison of coral reef fish communities between two fished and one protected reefs in New Caledonia South Lagoon Marine Park. *Cybium*, 29(2): 159-174.

Chesson J. (1978). Measuring preference in selective predation. *Ecology*, 59: 211-215.

Chesson J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology*, 64(5): 1297-1304.

Chittaro P.M. (2004). Fish-habitat associations across multiple spatial scales. *Coral Reefs*, 23: 235-244.

Choat J.H. & Robertson D.R. (2002). Age-based studies on coral reef fishes. In: Coral reef fishes: dynamics and diversity in a complex ecosystem (ed. Sale PF). pp. 57-80. Academic Press, San Diego.

Churcher-Hoffman T. (2001). Reefs of life to reefs of death: the political ecology of coral reef health in Fiji and the Cook Islands. Doctoral Thesis. Department of Geography. University of California. Berkeley. 333 pp.

Churcher-Hoffman T. (2002a). Coral reef health and effects of socio-economic factors in Fiji and Cook Islands. *Marine pollution bulletin*, 44: 1281-1293.

Churcher-Hoffman T. (2002b). The reimplementation of the Ra'ui: coral reef management in Rarotonga, Cook Islands. *Coastal Management*, 30: 401-418.

Claudet J., Osenberg C.W., Benedetti-Cecchi L., Domenici P., García-Charton J.-A., Perez-Ruzafa A., Badalamenti F., Bayle-Sempere J., Brito A., Bulleri F., Culioli J.-M., Dimech M., Falcon J.M., Guala I., Milazzo M., Sanchez-Meca J., Somerfield P.J., Stobart B., Vandeperre F., Valle C. & Planes S. (2008). Marine reserves: size and age do matter. *Ecology Letters*, 11(5): 481-489.

Claudet J., Pelletier D., Jouvenel J.Y., Bachet F. & Galzin R. (2006). Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a north-western Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation*, 130(3): 349-369.

Cole R.G., Ayling A.M. & Creese R.G. (1990). Effects of marine protection at Goat Island, northern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 24: 197-210.

Cole R.G., Syms C., Davey N.K., Gust N., Notman P., Stewart R., Radford C.A., Carbines G., Carr M.H. & Jeffs A.G. (2007). Does breathing apparatus affect fish counts and observations? A comparison at three New Zealand fished and protected areas. *Marine Biology*, 150: 1379–1395.

Côté I.M., Mosquera I. & Reynolds J.D. (2001). Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology*, 59((Supplement A)): 178-189.

Crawley M.J. (2007). The R book. John Wiley & Sons Ltd., Chichester. 942 pp.

Cucknell M.J. (2005). Description of physical substrate and coral composition around Rarotonga lagoon, Cook Islands. Masters Thesis. School of Ocean Sciences University of Wales. Bangor. 130 pp.

Dahlgren C.P. & Eggleston D.B. (2001). Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Marine Ecology-Progress Series*, 217: 145-156.

Diamant A. (1989). Ecology of the acanthocephalan *Sclerocollum rubrimaris* Schmidt and Paperna, 1978 (Rhadinorhynchidae: Gorgorhynchinae) from wild populations of rabbitfish (genus *Siganus*) in the northern Red Sea. *Journal of Fish Biology*, 34(3): 387-397.

Diamond J. (1975). The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, 7: 129-146.

Dominici-Arosemena A. & Wolff M. (2005). Reef fish community structure in Bocas del Toro (Caribbean, Panama): Gradients in habitat complexity and exposure. *Caribbean Journal of Science*, 41(3): 613-637.

Drumm D.J. (2004). Habitats and macroinvertebrate fauna of the reef-top of Rarotonga, Cook Islands: implications for fisheries and conservation management. Doctoral Thesis. Marine Science Department. University of Otago. Dunedin. 277 pp.

Dudas S.E., McGaw I.J. & Dower J.F. (2005). Selective crab predation on native and introduced bivalves in British Columbia. *Journal of Experimental Marine Biology and Ecology*, 325(1): 8-17.

Dufour V., Jouvenel J.Y. & Galzin R. (1995). Study of a Mediterranean reef fish assemblage - Comparisons of population-distributions between depths in protected and unprotected areas over one decade. *Aquatic Living Resources*, 8(1): 17-25.

Dugan J.E. & Davis G.E. (1993). Applications of marine refugia to coastal fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(9): 2029-2042.

Dulvy N.K., Freckleton R.P. & Polunin N.V. (2004a). Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters*, 7: 410-416.

Dulvy N.K., Polunin N.V.C., Mill A.C. & Graham N.A.J. (2004b). Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(3): 466.

Edgar G.J. & Barrett N.S. (1997). Short term monitoring of biotic change in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology*, 213(2): 261-279.

Edgar G.J. & Barrett N.S. (1999). Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology*, 242(1): 107-144.

Edgar G.J., Bustamante R.H., Farina J.M., Calvopina M., Martinez C. & Toral-Granda M.V. (2004). Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environmental Conservation*, 31(3): 212-218.

Edgar G.J., Samson C.R. & Barrett N.S. (2005). Species extinction in the marine environment: Tasmania as a regional Example of overlooked losses in biodiversity. *Conservation Biology*, 19(4): 1294-1300.

Egerton J. (2005). The abundance, distribution, and biomass of coral reef fish around the Rarotongan lagoon, Cook Islands. Masters Thesis. School of Ocean Sciences University of Wales. Bangor. 135 pp.

English S., Wilkinson C.R. & Baker V. (eds.) (1997). *Survey manual for tropical marine resources*. Australian Institute of Marine Science, Townsville. 390 pp.

Engqvist L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, 70(4): 967-971.

Evans R.D. & Russ G.R. (2004). Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 14: 505-519.

Fernandez-Duque E. (1997). Comparing and Combining Data across Studies: Alternatives to Significance Testing. *Oikos*, 79(3): 616-618.

Fernandez-Duque E. & Valeggia C. (1994). Meta-Analysis: A valuable tool in conservation research. *Conservation Biology*, 8(2): 555-561.

Floeter S.R., Halpern B.S. & Ferreira C.E.L. (2006). Effects of fishing and protection on Brazilian reef fishes. *Biological Conservation*, 128: 391-402.

Forrester G.E. (1990). Factors influencing the juvenile demography of a coral reef fish. *Ecology*, 71(5): 1666-1681.

Francour P., Harmelin J.G., Pollard D. & Sartoretto S. (2001). A review of marine protected areas in the north-western Mediterranean region: siting, usage, zonation and management. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 11(3): 155-188.

Friedlander A.M., Brown E. & Monaco M.E. (2007). Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Marine Ecology Progress Series*, 351: 221-233.

Friedlander A.M., Brown E.K., Jokiel P.L., Smith W.R. & Rodgers K.S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs*, 22(3): 291-305.

Friedlander A.M. & DeMartini E.E. (2002). Contrasts in density, size, and biomass of reef fishes between the north-western and the main Hawaiian islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*, 230: 253-264.

Froese R. & Pauly D. (eds.) (2008). FishBase. Online at http://www.fishbase.org. version (04/2008).

García-Charton J.A. & Perez Ruzafa A. (1999). Ecological heterogeneity and the evaluation of the effects of marine reserves. *Fisheries Research (Amsterdam)*, 42: 1-20.

Garcia S.M. & Newton C. (1997). Current situation, trends, and prospects in World capture fisheries. In: Global trends: fisheries management. (eds. Pikitch EK, Huppert DD & Sissenwine MP). pp. 3-27. American Fisheries Society Symposium 20, Bethesda.

Gell F. & Roberts C. (2002). The fishery effects of marine reserves and fishery closures. World Wildlife Fund - United States. 89 pp. (http://www.worldwildlife.org/oceans/fishery_effects.pdf)

Gerber L.R., Kareiva P.M. & Bascompte J. (2002). The influence of life history attributes and fishing pressure on the efficacy of marine reserves. *Biological Conservation*, 106: 11-18.

Gerber L.R., Botsford L.W., Hastings A., Possingham H.P., Gaines S.D., Palumbi S.R. & Andelman S. (2003). Population models for marine reserve design: A retrospective and prospective synthesis. *Ecological Applications*, 13(1): S47-S64.

Gibbs P.E., Stoddart D.R. & Vevers H.G. (1971). Coral reefs and associated communities in the Cook Islands. *Royal Society of New Zealand Bulletin*, 8(Cook Bicentenary Expedition in the South-West Pacific): 91-105.

Gillanders B., M. , Able K., W. , Brown J., A. , Eggleston D., B. & Sheridan P., F. (2003). Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series*, 247: 281-295.

Glynn P.W. (1973). Ecology of a Caribbean coral reef - *Porites* reef-flat biotope. II. Plankton Community with evidence for depletion. *Marine Biology*, 22(1): 1-21.

Goni R. (1998). Ecosystem effects of marine fisheries: an overview. *Ocean & Coastal Management*, 40(1): 37-64.

Graham N.A.J., Dulvy N.K., Jennings S. & Polunin N.V.C. (2005). Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. *Coral Reefs*, 24(1): 118.

Graham N.A.J., Evans R.D. & Russ G.R. (2003). The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environmental Conservation*, 30(2): 200-208.

Gratwicke B., Petrovic C. & Speight M.R. (2006). Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. *Environmental Biology of Fishes*, 76(2-4): 191-210.

Green R.H. (1979). Sampling design and statistical methods for environmental biologists. Wiley and Sons, New York. 257 pp.

Greig H. (2008). Students make Takitumu Lagoon Day a success. 11 June 2008. In: *Cook Islands News*. Rarotonga, Cook Islands.

Grigg R.W. (1994). Effects of sewage discharge, fishing pressure and habitat complexity on coral reef ecosystems and reef fishes in Hawaii. *Marine Ecology Progress Series*, 103: 25-34.

Guidetti P., Milazzo M., Bussotti S., Molinari A., Murenu M., Pais A., Spanò N., Balzano R., Agardy T., Boero F., Carrada G., Cattaneo-Vietti R., Cau A., Chemello R., Greco S., Manganaro A., Notarbartolo di Sciara G., Russo G.F. & Tunesi L. (2008). Italian marine reserve effectiveness: Does enforcement matter? *Biological Conservation*, 141(3): 699-709.

Guidetti P. & Sala E. (2007). Community-wide effects of marine reserves in the Mediterranean Sea. *Marine Ecology Progress Series*, 335: 43-56.

Gust N., Choat J.H. & McCormick M.I. (2001). Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Marine Ecology-Progress Series*, 214: 237.

Gust N. (2004). Variation in the population biology of protogynous coral reef fishes over tens of kilometres. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(2): 205-218.

Hairston N.G., Smith F.E. & Slobodkin L.B. (1960). Community Structure, Population Control, and Competition. *The American Naturalist*, 94(879): 421-425.

Halpern B.S. (2003). The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications*, 13(1): S117-S137.

Halpern B.S., Gaines S.D. & Warner R.R. (2004). Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecological Applications*, 14(4): 1248-1256.

Halpern B.S. & Warner R.R. (2002). Marine reserves have rapid and lasting effects. *Ecology Letters*, 5(3): 361-366.

Halpern B.S. & Warner R.R. (2003). Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society B-Biological Sciences*, 270: 1871-1878.

Hamner W.M., Colin P.L. & Hamner P.P. (2007). Export-import dynamics of zooplankton on a coral reef in Palau. *Marine Ecology-Progress Series*, 334: 83-92.

Hastings A. & Botsford L.W. (1999). Equivalence in yield from marine reserves and traditional fisheries management. *Science*, 284(5419): 1537-8.

Hastings A. & Botsford L.W. (2003). Comparing designs of marine reserves for fisheries and for biodiversity. *Ecological Applications*, 13(1): S65-S70.

Hawkins J.P., Roberts C.M., Dytham C., Schelten C. & Nugues M.M. (2006). Effects of habitat characteristics and sedimentation on performance of marine reserves in St. Lucia. *Biological Conservation*, 127: 487-499.

Hedges L.V., Gurevitch J. & Curtis P.S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80(4): 1150-1156.

Hedges L.V. & Olkin I. (1985). Statistical methods for meta-analysis. Academic Press Inc, San Diego. 369 pp.

Hilborn R., Stokes K., Maguire J.J., Smith T., Botsford L.W., Mangel M., Orensanz J., Parma A., Rice J., Bell J., Cochrane K.L., Garcia S., Hall S.J., Kirkwood G.P., Sainsbury K., Stefansson G. & Walters C. (2004). When can marine reserves improve fisheries management? *Ocean & Coastal Management*, 47(3-4): 197-205.

Holden B. (1992a). Circulation and flushing Ngatangiia Harbour and Muri Lagoon, Rarotonga, Cook Islands. SOPAC Technical Report. 52 pp.

Holden B. (1992b). Ocean currents and circulation, Avarua - Motutoa, Rarotonga, Cook Islands. . SOPAC Technical Report 143. 49 pp.

Holland K.N., Peterson J.D., Lowe C.G. & Wetherbee B.M. (1993). Movements, distribution and growth rates of the white goatfish *Mulloides flavolineatus* in a fisheries conservation zone. *Bulletin of Marine Science*, 52(3): 982-992.

Huedo-Medina T.B., Sanchez-Meca J., Marin-Martinez F. & Botella J. (2006). Assessing heterogeneity in meta-analysis: Q statistic or I-2 index? *Psychological Methods*, 11(2): 193-206.

Hughes T.P. (1994). Catastrophes, Phase-Shifts, and Large-Scale Degradation of a Caribbean Coral-Reef. *Science*, 265(5178): 1547.

Ivlev V.S. (1961). Experimental ecology of the feeding of fishes. Yale University Press, New Haven. 302 pp.

Jennings S., Boulle D.P. & Polunin N.V.C. (1996a). Habitat correlates of the distribution and biomass of Seychelles' reef fishes. *Environmental Biology of Fishes*, 46: 15-25.

Jennings S., Marshall S.S. & Polunin N.V.C. (1996b). Seychelles' marine protected areas: Comparative structure and status of reef fish communities. *Biological Conservation*, 75(3): 201.

Jennings S. & Polunin N.V. (1997). Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs*, 16: 71-82.

Jennings S. & Polunin N.V.C. (1996a). Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *Journal of Applied Ecology*, 33(2): 400.

Jennings S. & Polunin N.V.C. (1996b). Impacts of fishing on tropical reef ecosystems. *Ambio*, 25(1): 44-49.

Jennings S., Reynolds J.D. & Polunin N.V.C. (1999). Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conservation Biology*, 13(6): 1466-1475.

Johannes R.E. (1994). Pacific Island Peoples' Science and Marine Resource Management. In: Science of Pacific Island Peoples (eds. Morrison J, Geraghty P & Crowl L). pp. 81-89. Institute of Pacific Studies, Suva.

Johannes R.E. (1998). The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology & Evolution*, 13(6): 243-246.

Johannes R.E. (2002). The renaissance of community-based marine resource management in Oceania. *Annual Review of Ecology and Systematics*, 33: 317-340.

Jones G.P. (1986). Food availability affects growth in a coral reef fish. *Oecologia*, 70(1): 136-139.

Jones G.P. (1988). Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of 2 coral-reef fishes. *Journal of Experimental Marine Biology and Ecology*, 123(2): 115-126.

Jones G.P., Ferrell D.J. & Sale P.F. (1991). Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. In: The ecology of fishes on coral reefs (ed. Sale PF). pp. 156-179. Academic Press, San Diego.

Jones G.P. (1991). Post-recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: The ecology of fishes on coral reefs (ed. Sale PF). pp. 294-328. Academic Press, San Diego.

Kramer D.L. & Chapman M.R. (1999). Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, 55(1-2): 65-79.

Kritzer J.P. (2004). Effects of noncompliance on the success of alternative designs of marine protected-area networks for conservation and fisheries management. *Conservation Biology*, 18(4): 1021-1031.

Kulbicki M., Sarramegna S., Letourneur Y., Wantiez L., Galzin R., Mou-Tham G., Chauvet C. & Thollot P. (2007). Opening of an MPA to fishing: Natural variations in the structure of a coral reef fish assemblage obscure changes due to fishing. *Journal of Experimental Marine Biology and Ecology*, 353(2): 145-163.

La Mesa G., Di Muccio S. & Vacchi M. (2006). Structure of a Mediterranean cryptobenthic fish community and its relationships with habitat characteristics. *Marine Biology*, 149(2): 149-167.

Langlois T., Anderson M., Babcock R. & Kato S. (2006). Marine reserves demonstrate trophic interactions across habitats. *Oecologia*, 147(1): 134-140.

Lassig B.R. (1983). The effects of a cyclonic storm on coral reef fish assemblages. *Environmental Biology of Fishes*, 9(1): 55-63.

Lawton J.H. (1994). What Do Species Do in Ecosystems? *Oikos*, 71(3): 367-374.

Lecchini D. & Galzin R. (2005). Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Marine Biology*, 147(1): 47-58.

Legendre P. (2001). Model II regression – User's guide. Département de sciences biologiques, Université de Montréal.

Leslie D.M. (1980). Soils of Rarotonga, Cook Islands. New Zealand Soil Survey Report. 49. 68 pp.

Lessios H.A. (1988). Mass Mortality of Diadema Antillarum in the Caribbean: What Have We Learned? *Annual Review of Ecology and Systematics*, 19(1): 371-393.

Lewis J.B. (1977). Processes of organic production on coral reefs. *Biological Reviews*, 52(3): 305-347.

Lieske E. & Myers R. (2002). Coral reef fishes. First revised edition. Princeton University Press, Princeton, New Jersey. 400 pp.

Light P.R. & Jones G.P. (1997). Habitat preference in newly settled coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs*, 16(2): 117-126.

Lincoln-Smith M.P., Pitt K.A., Bell J.D. & Mapstone B.D. (2006). Using impact assessment methods to determine the effects of a marine reserve on abundances and sizes of valuable tropical invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(6): 1251-1266.

Lockwood D.R., Hastings A. & Botsford L.W. (2002). The effects of dispersal patterns on marine reserves: does the tail wag the dog? *Theoretical Population Biology*, 61(3): 297-309.

Macpherson E. (1998). Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *Journal of Experimental Marine Biology and Ecology*, 220(1): 127-150.

Malvadkar U. & Hastings A. (2008). Persistence of mobile species in marine protected areas. *Fisheries Research*, 91(1): 69-78.

Manarangi-Trott L. (2000). Maito (*Ctenochaetus striatus*): its age and growth characteristics and the effects of fishing pressure in Rarotonga, Cook Islands. Honours Thesis. School of Biological, Earth and Environmental Sciences. University of New South Wales. Sydney. 30 pp.

Manly B.F.J. (1974). A model for certain types of selection experiments. *Biometrics*, 30: 281-294.

Manly B.F.J. (1993). Comments on design and analysis of multiple-choice feeding-preference experiments. *Oecologia*, 93: 149-152.

Manly B.F.J., McDonald L.L., Thomas D.L., McDonald T.L. & Erickson W.P. (2002). Resource selection by animals: statistical design and analysis for field studies. 2nd edn. Kluwer Academic Publishers, Dordrecht, Netherlands. 221 pp.

Martell S.J.D., Essington T.E., Lessard B. & Kitchell J.F. (2005). Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(6): 1320.

Matthews E., Veitayaki J. & Bidesi V.R. (1998). Fijian villagers adapt to changes in local fisheries. *Ocean and Coastal Management*, 38(3): 207-224.

May J.J. (2005). The distribution and abundance of key invertebrate species in the Rarotonga lagoon, Cook Islands. School of Ocean Sciences University of Wales. Bangor. 66 pp.

McArdle B.H. & Anderson M.J. (2001). Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82: 290-297.

McClanahan T.R. (1994). Kenyan coral reef lagoon fish: Effects of fishing, substrate complexity, and sea urchins. *Coral Reefs*, 13(4): 231-241.

McClanahan T.R. & Arthur R. (2001). The effect of marine reserves and habitat on populations of east African coral reef fishes. *Ecological Applications*, 11(2): 559-569.

McClanahan T.R., Graham N., A. J., Calnan J., M. & MacNeil M.A. (2007). Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications*, 17(4): 1055-1067.

McClanahan T.R., Marnane M.J., Cinner J.E. & Kiene W.E. (2006). A comparison of marine protected areas and alternative approaches to coral-reef management. *Current Biology*, 16(14): 1408-1413.

McClanahan T.R., Muthiga N.A., Kamukuru A.T., Machano H. & Kiambo R.W. (1999). The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biological Conservation*, 89(2): 161-182.

McCormack G. (2007). Cook Islands Biodiversity Database. Version 2007.2. Cook Islands Natural Heritage Trust, Rarotonga. Online at http://cookislands.bishopmuseum.org. Date accessed: 18th April 2008.

Mead S.M. (ed.) (1984). *Customary concepts of the Maori: a source book for Maori Studies students*. Victoria University of Wellington, Wellington.

Meester G.A., Mehrotra A., Ault J.S. & Baker E.K. (2004). Designing marine reserves for fishery management. *Management Science*, 50(8): 1031-1043.

Meyer C.G. (2003). An empirical evaluation of the design and function of a small marine reserve (Waikiki Marine Life Conservation District). Doctoral dissertation. Zoology Department. University of Hawai'i at Manoa. 143 pp.

Meyer C.G. & Holland K.N. (2005). Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes*, 73(2): 201-210.

Meyer J., Steinhauser J., Jeltsch F. & Brandl R. (2007). Large trees, acacia shrubs, and the density of *Thallomys nigricauda* in the Thornveld savannah of South Africa. *Journal of Arid Environments*, 68(3): 363-370.

Micheli F., Benedetti-Cecchi L., Gambaccini S., Bertocci I., Borsini C., Osio G.C. & Roman F. (2005). Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecological Monographs*, 75(1): 81-102.

Micheli F., Halpern B.S., Botsford L.W. & Warner R.R. (2004). Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications*, 14(6): 1709-1723.

Milazzo M., Badalamenti F., Vega Fernandez T. & Chemello R. (2005). Effects of fish feeding by snorkellers on the density and size distribution of fishes in a Mediterranean marine protected area. *Marine Biology*, 146: 1213-1222.

Moberg F. & Folke C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, 29(2): 215-233.

Moore J. (2006). Seafood consumption survey: Rarotonga. Diploma in Marine Studies Year Two Marine Reporting Projects. Bay of Plenty Polytechnic. 32 pp.

Mosquera I., Côté I.M., Jennings S. & Reynolds J.D. (2000). Conservation benefits of marine reserves for fish populations. *Animal Conservation*, 3: 321-332.

Munro J.L. & Williams D.M. (1985). Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. In: Vol. 4, Proceedings of the Fifth International Coral Reef Congress. pp. 545-572. Antenne Museum, Tahiti, French Polynesia.

Murty V.S. (2002). Marine ornamental fish resources of Lakshadweep. CMFRI Indian Council for Agricultural Research, India Cochin. 384pp.

Myers R.A. & Worm B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423(6937): 280-283.

Myers R.F. (1999). Micronesian reef fishes: a comprehensive guide to the coral reef fishes of Micronesia. Coral Graphics, Guam. 522 pp.

Nakagawa S. & Cuthill I.C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, 82(4): 591-605.

Nardi K., Jones G.P., Moran M.J. & Cheng Y.W. (2004). Contrasting effects of marine protected areas on the abundance of two exploited reef fishes at the sub-tropical Houtman Abrolhos Islands, Western Australia. *Environmental Conservation*, 31(2): 160-168.

Neu C., Byers C. & Peek J. (1974). A technique for analysis of utilization-availability data. *Journal of Wildlife Management*, 38: 541-5.

Neubert M.G. (2003). Marine reserves and optimal harvesting. *Ecology Letters*, 6: 843-849.

Ojeda-Martinez C., Bayle-Sempere J., Sánchez-Jerez P., Forcada A. & Valle C. (2007). Detecting conservation benefits in spatially protected fish populations with meta-analysis of long-term monitoring data. *Marine Biology*, 151(3): 1153-1161.

Osenberg C.W., Bolker B.M., White J.S., St Mary C.M. & Shima J.S. (2006). Statistical issues and study design in ecological restorations: lessons learned from marine reserves. In: Foundations of Restoration Ecology (eds. Falk DA, Palmer MA & Zedler JB). pp. 280-302. Island Press.

Osenberg C.W., Sarnelle O., Cooper S.D. & Holt R.D. (1999). Resolving ecological questions through meta-analysis: goals, metrics and models. *Ecology*, 80(4): 1105-1117.

Osenberg C.W. & Schmitt R.J. (1996). Detecting ecological impacts caused by human activities. In: Detecting ecological impacts: concepts and applications in coastal habitats (eds. Schmitt RJ & Osenberg CW). pp. 3-16. Academic Press, San Diego.

Osenberg C.W., Schmitt R.J., Holbrook S.J., Abu-Saba K.E. & Flegal A.R. (1996). Detection of environmental impacts. In: Detecting ecological impacts: concepts and applications in coastal habitats (eds. Schmitt RJ & Osenberg CW). pp. 83-108. Academic Press, San Diego.

Overton J. & Thaman R.R. (1999). Resources and the Environment. In: Strategies for Sustainable Development: Experiences from the Pacific (eds. Overton J & Scheyvens R). pp. 19-32. University of New South Wales Press, Sydney.

Palumbi S.R. (2001). The ecology of marine protected areas. In: Marine community ecology (eds. Bertness MD, Gaines SD & Hay ME). pp. 509-530. Sinauer Associates Inc., Sunderland, Massachusetts.

Palumbi S.R. (2004). Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. *Annual Review of Environment and Resources*, 29: 31-68.

Parnell P.E., Dayton P.K., Lennert-Cody C.E., Rasmussen L.L. & Leichter J.J. (2006). Marine reserve design: optimal size, habitats, species affinities, diversity, and ocean microclimate. *Ecological Applications*, 16(3): 945-962.

Parnell P.E., Lennert-Cody C.E., Geelen L., Stanley L.D. & Dayton P.K. (2005). Effectiveness of a small marine reserve in southern California. *Marine Ecology Progress Series*, 296: 39-52.

Parrish J.D. (1989). Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series*, 58(1-2): 143-160.

Passfield K. & Tiraa A. (1998). Management Plan for a Ra'ui in Avana-Aroko-Nukupure. Koutu Nui. Rarotonga.

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres F.J. (1998). Fishing down marine food webs. *Science*, 279: 860-863.

Pauly D., Christensen V., Guenette S., Pitcher T.J., Sumaila U.R., Walters C.J., Watson R. & Zeller D. (2002). Towards sustainability in world fisheries. *Nature*, 418: 689-695.

Pinnegar J.K., Polunin N.V.C., Francour P., Badalamenti F., Chemello R., Harmelin-Vivien M.L., Hereu B., Milazzo M., Zabala M., D'Anna G. & Pipitone C. (2000). Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation*, 27(2): 179-200.

PISCO (2007). The science of marine reserves. Partnership for interdisciplinary studies of coastal oceans. (2nd Edition, United States Version). 22pp.

Pitcher T.J. (2001). Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. *Ecological Applications*, 11(2): 601-617.

Pledger S., Geange S., Hoare J. & Pérez Matus A. (2007). Resource selection: tests and estimation using null models. *Research Report Series, School of Mathematics, Statistics and Computer Science*. Victoria University of Wellington. Wellington. 22 pp. (Access at http://www.mcs.vuw.ac.nz/research/publications/reports/mscs/mscs07-04.pdf)

Polunin N.V.C. & Roberts C.M. (1993). Greater biomass and value of target coral-reef fishes in two small Carribean marine reserves. *Marine Ecology Progress Series*, 100: 167-176.

Ponia B. & Raumea K. (1998). Rarotonga marine reserve baseline assessment: Nikao ra'ui, Aroko ra'ui, Matavera ra'ui, Tikioki ra'ui and Rutaki ra'ui. Ministry of Marine Resources, Government of the Cook Islands. Miscellaneous Report. 98/05. 18 pp.

Ponia B., Raumea K. & Turua T. (1998). 1st monitoring survey of the Rarotonga Ra'ui. Ministry of Marine Resources, Government of the Cook Islands. Miscellaneous report. 99/18. 27 pp.

Popham E. (1944). A study of the changes in an aquatic insect population using minnows as the predators. *Proceedings of the Zoological Society of London*, A114: 74-81.

Quinn G.P. & Keough M.J. (2002). Experimental design and data analysis for biologists. Cambridge University Press, Cambridge. 537 pp.

R Development Core Team (2006). R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. http://www.R-project.org.

Randall J.E. (1965). Food habits of reef fishes of the West Indies. In: International conference on tropical oceanography. pp. 665-847. University of Miami Institute of Marine Sciences, Miami Beach, Florida.

Randall J.E. (2005). Reef and shore fishes of the South Pacific. New Caledonia to Tahiti and the Pitcairn Islands. University of Hawaii Press, Honolulu. 707 pp.

Raumea K., Turua T., Makikiriti N., Marurai J. & Ponia B. (2000a). Rarotonga marine reserve baseline assessment of Aroa Ra'ui. Ministry of Marine Resources, Government of the Cook Islands.

Raumea K., Turua T., Makikiriti N., Rongo T., Roi N. & Ponia B. (2000b). 2nd monitoring survey of the Rarotonga Ra'ui. Ministry of Marine Resources, Government of the Cook Islands. Miscellaneous report. 27 pp.

Roberts C.M. (1995a). Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology*, 9(5): 988-995.

Roberts C.M. (1995b). Rapid Build-up of Fish Biomass in a Caribbean Marine Reserve. *Conservation Biology*, 9(4): 815-826.

Roberts C.M. (1997). Connectivity and management of Caribbean coral reefs. *Science*, 278: 1454-1457.

Roberts C.M., Bohnsack J.A., Gell F., Hawkins J.P. & Goodridge R. (2001). Effects of marine reserves on adjacent fisheries. *Science*, 294(5548): 1920-1923.

Roberts C.M. & Polunin N.V.C. (1991). Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries*, 1(1): 65-91.

Roberts C.M. & Polunin N.V.C. (1992). Effects of marine reserve protection on Northern Red Sea fish populations. In: Proceedings of the seventh international coral reef symposium 22-27 June 1992 (ed. Richmond RH). pp. 969-977, Guam, Micronesia.

Roberts C.M. & Polunin N.V.C. (1993). Marine reserves: Simple solutions to managing complex fisheries? *Ambio*, 22(6): 363-368.

Rochet M.-J. (1998). Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science*, 55(3): 371-391.

Rochet M.-J. & Trenkel V.M. (2003). Which community indicators can measure the impact of fishing? A review and proposals. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(1): 86.

Roughgarden J., Gaines S. & Possingham H. (1988). Recruitment dynamics in complex life cycles. *Science*, 241(4872): 1460-1466.

Rowley R.J. (1994). Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 4(3): 233-254.

Russ G.R. (2002). Yet another review of marine reserves as reef fishery management tools. In: Coral reef fishes; dynamics and diversity in a complex ecosystem (ed. Sale PF). pp. 421-443. Academic Press.

Russ G.R. & Alcala A.C. (1996). Marine Reserves: Rates and Patterns of Recovery and Decline of Large Predatory Fish. *Ecological Applications*, 6(3): 947-961.

Russ G.R. & Alcala A.C. (1998a). Natural fishing experiments in marine reserves 1983-1993: community and trophic responses. *Coral Reefs*, 17(4): 383-397.

Russ G.R. & Alcala A.C. (1998b). Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. *Coral Reefs*, 17(4): 399-416.

Sala E., Aburto-Oropeza O., Paredes G., Parra I., Barrera J.C. & Dayton P.K. (2002). A general model for designing networks of marine reserves. *Science*, 298(5600): 1991-3.

Sale P.F. (2002). The science we need to develop for more effective management. In: Coral Reef Fishes; Dynamics and Diversity in a Complex Ecosystem (ed. Sale PF). pp. 361-376. Academic Press, San Diego.

Sale P.F., Cowen R.K., Danilowicz B.S., Jones G.P., Kritzer J.P., Lindeman K.C., Planes S., Polunin N.V., Russ G.R. & Sadovy Y.J. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution*, 20(2): 74-80.

Salomon A.K., Waller N.P., McIlhagga C., Yung R.L. & Walters C. (2002). Modeling the trophic effects of marine protected area zoning policies: A case study. *Aquatic Ecology*, 36(1): 85-95.

Samoilys M. (1988). Abundance and species richness of coral reef fish on the Kenyan coast: the effects of protective management and fishing. In: Proceedings of the 6th International Coral Reef Symposium (eds. Choat JH, D. Barnes, MA. Borowitzka, J.C. Coll, P.J.Davies, P. Flood, B.G. Hatcher, D. Hopley, P.A. Hutchings, D. Kinsey, G.R. Orme, M. Pichon, P.F. Sale, P. Sammarco, C.C. Wallace, C. Wilkinson, Wolanski E & Bellwood O). pp. 261-266, Townsville, Australia.

Samoilys M.A. & Carlos G. (2000). Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes*, 57(3): 289-304.

Samoilys M.A., Martin-Smith K.M., Giles B.G., Cabrera B., Anticamara J.A., Brunio E.O. & Vincent A.C.J. (2007). Effectiveness of five small Philippines' coral reef reserves for fish populations depends on site-specific factors, particularly enforcement history. *Biological Conservation*, 136(4): 584-601.

Samou S. (1999). Marine Resources. In: Strategies for Sustainable Development: Experiences from the Pacific (eds. Overton J & Scheyvens R). pp. 142-154. University of New South Wales Press, Sydney.

Sanchez-Lizaso J.L., Goni R., Renones O., García Charton J.A., Galzin R., Bayle J.T., Sanchez Jerez P., Perez Ruzafa A. & Ramos A.A. (2000). Density Dependence in marine protected populations: a review. *Environmental Conservation*, 27(2): 144-158.

Saywood A., Turua T. & Makikiriti N. (2002). 3rd monitoring survey of the Rarotonga Ra'ui. Ministry of Marine Resources, Government of the Cook Islands. Miscellaneous Report. 2002/01. 29 pp.

Searcy S.P., Eggleston D.B. & Hare J.A. (2007). Environmental influences on the relationship between juvenile and larval growth of Atlantic croaker *Micropogonias undulatus*. *Marine Ecology-Progress Series*, 349: 81-88.

Shaddish W.R. & Haddock C.K. (1994). Combining estimates of effect size. In: The handbook of research synthesis (eds. Cooper H & Hedges LV). pp. 261-281. Russell Sage Foundation, New York.

Shears N. & Babcock R. (2003). Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series*, Vol. 246: 1-16.

Shears N.I. & Babcock R.C. (2002). Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, 132(1): 131-142.

Shears N.T., Grace R.V., Usmar N.R., Kerr V. & Babcock R.C. (2006). Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. *Biological Conservation*, 132(2): 222-231.

Shepherd S.A. & Brook J.B. (2007). Distribution and ontogenetic shifts in habitat and abundance of the temperate western blue groper, *Achoerodus gouldii* (Richardson). *Journal of Fish Biology*, 71(5): 1457-1478.

Siegel S. & Castellan N.J. (1988). Nonparametric statistics for the behavioural sciences. McGraw Hill, New York. 399 pp.

Sosa-Lopez A., Mouillot D., Do Chi T. & Ramos-Miranda J. (2005). Ecological indicators based on fish biomass distribution along trophic levels: an application to the Terminos coastal lagoon, Mexico. *ICES Journal of Marine Science*, 62(3): 453-458.

SPC (2007). Reef fisheries observatory: fieldwork and surveys in the Cook Islands. In: *Fisheries Newsletter*, pp. 2-7.

SPREP (2001). Outcomes of the WSSD Pacific Regional Multi-stakeholder consultation, 5-7 September 2001. Pacific Region Submission to the World Wide Summit on Sustainable Development.

SPSS Inc. (2008). SPSS for Windows. Release 16.0.0. SPSS Inc. Chicago.

Statistics Office, Cook Islands (2006). Rarotonga total population by census districts and age groups. Online at http://www.stats.gov.ck/Statistics/CensusSurveys/census06/Cen06-Tab6.pdf. Date accessed: May 31 2008.

Stearns S.C. & Crandall R.E. (1984). Plasiticity for age and size at sexual maturity: a life-history response to unavoidable stress. In: Fish reproduction: strategies and tactics (eds. Potts GW & Wootton RJ). pp. 13-33. Academic Press, London.

Stewart-Oaten A., Murdoch W.W. & Parker K.R. (1986). Environmental Impact Assessment: "Pseudoreplication" in Time? *Ecology*, 67(4): 929-940.

Sumaila U.R., Guenette S., Alder J. & Chuenpagdee R. (2000). Addressing ecosystem effects of fishing using marine protected areas. *ICES Journal of Marine Science*, 57(3): 752-760.

Taniera T. (1994). Traditional fisheries in Kiribati: survival and sustainability. In: Science of Pacific Island Peoples (eds. Morrison J, Geraghty P & Crowl L). pp. 113-120. Institute of Pacific Studies.

Tiraa A. (2006). Ra'ui in the Cook Islands - today's context in Rarotonga. *SPC Traditional Marine Resource Management and Knowledge Information Bulletin*, 19: 11-15.

Tuya F.C., García-Diez C., Espino F. & Haroun R.J. (2006). Assessment of the effectiveness of two marine reserves in the Canary Islands (eastern Atlantic). *Ciencias Marinas*, 32(3): 505–522.

Tuya F.C., Soboil M.L. & Kido J. (2000). An assessment of the effectiveness of Marine Protected Areas in the San Juan Islands, Washington, USA. *ICES Journal of Marine Science*, 57(4): 1218-1226.

Uiblein F. (2007). Goatfishes (Mullidae) as indicators in tropical and temperate coastal habitat monitoring and management. *Marine Biology Research*, 3(5): 275-288.

Uthicke S. & Benzie J.A.H. (2000). Effect of beche-de-mer fishing on densities and size structure of *Holothuria nobilis* (Echinodermata: Holothuroidea) populations on the Great Barrier Reef). *Coral Reefs*, 19: 271-276.

Veitayaki J. (1998). Traditional and community-based marine resources management system in Fiji: An evolving integrated process. *Coastal Management*, 26(1): 47-60.

Walsh W.J. (1983). Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs*, 2(1): 49-63.

Wantiez L., Thollot P. & Kulbicki M. (1997). Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs*, 16(4): 215-224.

Warner R.R. (1991). The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. In: The ecology of fishes on coral reefs (ed. Sale PF). pp. 387-398. Academic Press, San Diego.

Watson D.L., Harvey E.S., Kendrick G.A., Nardi K. & Anderson M.J. (2007). Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. *Marine Biology*, 152(5): 1197-1206.

Watson R. & Pauly D. (2001). Systematic distortions in world fisheries catch trends. *Nature*, 414: 534-536.

Westera M., Lavery P. & Hyndes G. (2003). Differences in recreationally targeted fishes between protected and fished areas of a coral reef marine park. *Journal of Experimental Marine Biology and Ecology*, 294(2): 145-168.

Williams D.M. & Sale P.F. (1981). Spatial and temporal patterns of recruitment of juvenile coral-reef fishes to coral habitats within One Tree Lagoon, Great Barrier Reef. *Marine Biology*, 65(3): 245-253.

Williams G.C. (1966). Adaptation and natural selection. A critique of some current evolutionary thought. Princeton University Press, Princeton. 307 pp.

Williamson D.H., Russ G.R. & Ayling A.M. (2004). No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environmental Conservation*, 31(2): 149-159.

Willis T.J. & Anderson M., J. (2003). Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Marine Ecology Progress Series*, 257: 209-221.

Willis T.J., Millar R.B., Babcock R.C. & Tolimieri N. (2003). Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environmental Conservation*, 30(2): 97-103.

Wolanski E. & Delesalle B. (1995). Upwelling by internal waves, Tahiti, French Polynesia. *Continental shelf research*, 15(2-3): 357-368.

Wood B.L., Hay R.F. & Brothers R.N. (1970). Geology of the Cook Islands. 103 pp.

Young E. (2004). Taboos could save the seas. In: *New Scientist*, 17 April 2004. p. 9.

Zeller D., Stoute S.L. & Russ G.R. (2003). Movements of reef fishes across marine reserve boundaries: Effects of manipulating a density gradient. *Marine Ecology Progress Series*, 254: 269-280.